A Revision of the Miocene Hominoidea of East Africa

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Synopsis

Seven species of Lower Miocene apes belonging to the Pongidae and Hylobatidae are revised. Each species is described in detail based on previously-described material and on 368 new specimens from Kenya, and diagnoses are emended to take into account the greater variability now seen to be present in each species.

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The African Dryopithecinae (Pongidae) are divided into two genera, *Proconsul* and *Limnopithecus*. The former is subdivided into two subgenera, *Proconsul* and *Rangwapithecus*, which differ from each other in morphology but overlap in size. The species within each subgenus are distinguished mainly on size. *Limnopithecus* is represented by the single species *L. legetet* Hopwood. The Hylobatidae has only one genus and species, *Dendropithecus macinnesi* (Le Gros Clark & Leakey), which was formerly grouped with *Limnopithecus*. A new subspecies *D. macinnesi songhorensis* is described.

Two of the species of fossil ape are present in basal Miocene deposits at least 22 m.y. old, and one of these and two others survive until the Middle Miocene, about 14 m.y. old. Proposed relationships of *Proconsul* and *Dendropithecus* with the Oligocene primates *Aegyptopithecus* and *Propliopithecus* are supported by the new specimens. The connection between the African Lower to Middle Miocene species and the Eurasian Middle Miocene species are not clear, although there is some evidence for a *Proconsul major–Sivapithecus indicus* link. It is not considered possible to postulate any direct connection between the Miocene and present-day apes, with the possible exception of *Dendropithecus macinnesi* leading to the gibbons.

Introduction

Early Miocene deposits in western Kenya were first discovered in 1909 when G. R. Chesnaye found fossils at Koru and Karungu (Andrews 1911). The first fossil ape specimens were not found until some time later, when Dr H. L. Gordon collected one specimen from Koru in 1926 (Hopwood 1933). The two most prolific Miocene sites in Kenya, Songhor and Rusinga Island, were discovered by Drs L. S. B. Leakey and D. G. MacInnes in 1931–32, and sporadic collecting at these sites (Leakey 1943; MacInnes 1943) was eventually succeeded by the British–Kenya Miocene Expeditions of 1947–51 organized by W. E. Le Gros Clark in England and L. S. B. Leakey in Kenya (Clark & Leakey 1950, 1951; Clark 1950; Leakey & Clark 1955). After the end

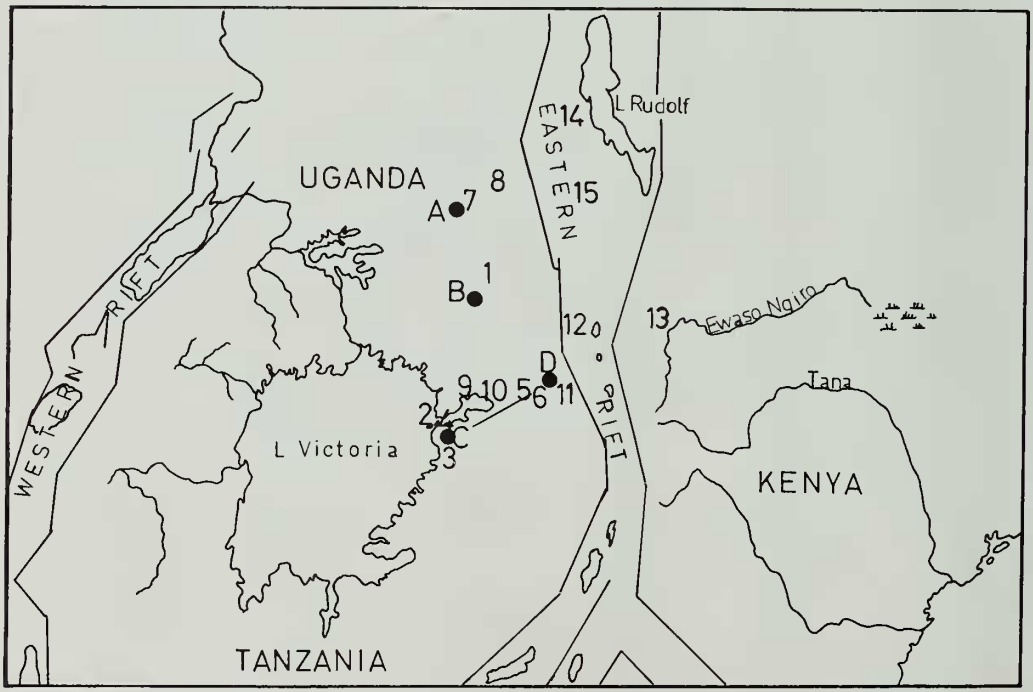

Fig. 1 Locality map of East Africa. Fossil localities: 1 Bukwa, 2 Mfwangano Island, 3 Karungu, 4 Rusinga Island, 5 Songhor, 6 Koru, 7 Napak, 8 Moroto, 9 Ombo, 10 Maboko Island, 11 Fort Ternan, 12 Ngorora, 13 Kirimon, 14 Losidok and Moruorot, 15 Loperot. Miocene Volcanoes: A Napak, B Elgon, C Kisingiri, D Tinderet.

of these expeditions work was continued on an individual basis by L. S. B. Leakey and others (Whitworth 1953, 1961; Leakey 1968; Van Couvering & Miller 1969; Andrews 1970, 1974; Andrews & Van Couvering 1975). A summary of Miocene field work up to the end of 1974 is given in Appendix I (p. 213), and numbers of specimens of hominoid primate found in Appendix II (p. 215). Fossil localities are shown in Fig. 1.

Up to the present time a total of 840 specimens of fossil hominoid primates has been recovered from the Early Miocene deposits of Kenya. Of these 644 represent cranial or dental fragments and are the subject of the present study. Some of the earlier discoveries (276 specimens) have been described previously (Hopwood 1933; MacInnes 1943; Clark & Leakey 1951; Clark & Thomas 1951; Clark 1952; Napier & Davis 1959; Leakey 1967, 1968; Andrews 1970, 1974). The remaining 368 specimens are described for the first time here and in Andrews (1973). A summary of specimens available for study is given in Appendix II (p. 215), and a list of the specimen field numbers used by earlier workers, with their permanent accession numbers used here, is given in Appendix III (p. 216).

Measuring techniques and abbreviations

Measurements were taken with a Helios dial caliper and recorded to the nearest 0·1 mm. All measurements were done at least twice, and a number of representative specimens were measured every 2–3 months. Over a period of 3 years the average measurement error was 1·1 %. The definitions of the measurements are given below. Points on the maxilla and mandible are as defined by Trevor (1950).

Description of measurements

MAXILLA

Naso–alv. ht	distance between nasospinale and alveolare.
Nasal aperture ht	distance between nasopinale and the top of the nasal aperture.
Nasal ht	distance between nasospinale and nasion.
Zyg. arch position	tooth above which the root of the zygomatic process of the maxilla is positioned.
Zyg. arch ht	distance between the cervical border of the crown of the corresponding tooth and the point of maximum angulation of the zygomatic process of the maxilla.
max. sinus L	maximum anteroposterior length of the floor of the maxillary sinus.
max. sinus B	maximum breadth of the floor of the maxillary sinus.
pal. b at M2 (ext)	external distance between the buccal borders of left and right M2.
Palate L	distance between the posterior (lingual) margins of the central incisors and the distal margins of the third molars.
Palate B at C	internal distance between lingual borders of the crown bases of left and right C.
Palate B at M2	internal distance between lingual borders of the crown bases of left and right M2.
Palate depth at C–P3	depth of palate above cervical borders of crowns of average of C and P3.
Palate depth at M2	depth of palate above cervical borders of crowns of M2.
M1–M3	molar tooth row chord.
P3–M3	premolar–molar tooth row chord.
C–M3	canine–premolar–molar tooth row chord.

MANDIBLE

Symph. d	maximum length along the mandibular symphysis.
Symph. t	minimum breadth across the mandibular symphysis.
P4 d	vertical depth of the mandibular body at the level of P4.
P4 t	perpendicular breadth of the mandibular body at the level of P4.
M2 d	vertical depth of the mandibular body at the level of M2.
M2 t	perpendicular breadth of the mandibular body at the level of M2.
I–I	distance between the most lingual points of the crown bases of the left and right lateral incisors.
C–C	distance between the most lingual points of the crown bases of the left and right canines.
P4–P4	distance between the most lingual points of the crown bases of the left and right fourth premolars.
M3–M3	distance between the most lingual points of the crown bases of the left and right third molars

INCISORS

md	maximum mesiodistal length.
md incis	mesiodistal length across the incisive edge.
md root	mesiodistal length across the root.
bl	buccolingual length.
buc ht	maximum height of the crown measured buccally.
$\frac{\text{md incis}}{\text{md}} \times 100$	index measuring the relative size of the incisive edge on the crown.

CANINES

max l	maximum length dimension measured along the long axis of the tooth.
perp b	minimum breadth measured perpendicular to the axis of maximum length.
buc ht	maximum height of the crown measured buccally.
mes ht ($\overline{C}$)	height of the crown at its most mesial point.
mes ridge ($\overline{C}$)	length of the mesial ridge from the top of the cingulum to the tip of the crown.
$\frac{\text{ridge}}{\text{mes ht}} \times 100$	index measuring the symmetry of the crown; a short ridge and low index indicates a highly asymmetrical crown.

LOWER P3

max l	as for canine.
perp b	as for canine.
buccal ht mes	maximum height of the crown measured from the most inferior point of the enamel extension on the mesial root to the tip of the crown.
buccal ht dist	the minimum height from the base of the crown on the distal root to the tip of the crown.
$\frac{\text{dist}}{\text{mes}} \times 100$	index measuring the extension of the enamel down the mesial root.

UPPER PREMOLARS

md	mesiodistal length along the central axis of the crown.
md buc (P3)	maximum mesiodistal length along the buccal edge of the crown.
bl	maximum buccolingual breadth.
buc ht	maximum height of the buccal cusp measured buccally.
ling ht	maximum height of the lingual cusp measured lingually.
$\frac{\text{md}}{\text{md buc}} \times 100$	index measuring the relative buccal extension of the crown.
$\frac{\text{buc ht}}{\text{ling ht}} \times 100$	index measuring the relative projection of the buccal cusp below the lingual one.

UPPER MOLARS

md	mesiodistal length along the central axis of the crown.
bl	maximum buccolingual breadth.
$\frac{\text{md}+\text{bl}}{2}$	the crown module, the 'average dimension' of the crown (Schuman & Brace 1954).
$\frac{\text{M2}}{\text{M1}} \times 100$	index measuring the relative size difference between M2 and M1.

LOWER MOLARS AND P4

md	mesiodistal length along the central axis of the crown.
bl mes	maximum buccolingual breadth across the trigonid.
bl dist	maximum buccolingual breadth across the talonid.
$\frac{\text{md}+\text{bl}}{2}$	as for upper molars.
$\frac{\text{M2}}{\text{M1}} \times 100$	as for upper molars.

AGE CLASSES (deposit data; see p. 215)

1	deciduous dentition
2	mixed dentition or isolated unerupted crowns
3	unworn permanent dentition
4	slightly worn permanent dentition
5	moderately worn permanent dentition
6	heavily worn permanent dentition

Other abbreviations

BM(NH)	British Museum (Natural History). Specimens from this Museum are indicated by the single-letter prefix, M.
KNM	Kenya National Museum. Specimens from this Museum are usually designated by a two-letter prefix, indicating the site of origin as follows:
KA	Karungu
KO	Koru
LS	Losidok
MB	Maboko
MO	Moruorot
MW	Mfwangano Island (Site numbers, where known, are indicated by M A, M B, etc.)
OM	Ombo
RU	Rusinga Island (Site numbers, where known, are indicated by R 1, R 2, etc.)
SO	Songhor (Site numbers, where known, are indicated by S 1, S 2, etc.)
WF	Williams Flat
UM–P	Uganda Museum.
YPM	Yale Peabody Museum.

Univariate statistics

In the table of measurements, the mean and number of specimens are given for each tooth. Where the sample size is nearly or greater than ten the following additional statistics are given:

S.D.	standard deviation
Coef. var.	coefficient of variation
S.E.	standard error
95% conf. limits	95% confidence limits.

Calculations were made on the Olivetti desk computer at the Department of Physiology, University of Nairobi.

Multivariate statistics

The method used is that of principal components analysis (Andrews & Williams 1973). It is explained in detail in that paper and in my honours dissertation for the Department of Physical Anthropology, Cambridge (Andrews 1973). The programme used was written by D. B. Williams and it was run on the Cambridge University Titan computer.

The data were divided into three sets for analysis in the computer. These were as follows:

(a) measurements of anterior dentition I1–C and anterior mandibular dimensions and symphysis (22 measurements).

(b) measurements of 'sectorial' dentition C–P4 and mandibular dimensions of this region (28 measurements).

(c) measurements of post-canine teeth P4–M3 and mandibular dimensions of this region (32 measurements).

This division was partly dictated by what measurements were available in the samples of fossil species. The analysis of the post-canine region is based on relatively large samples with few estimated values, and hence it is more reliable than that of the anterior dentition and symphysis which is based on small samples. The grouping was also made on functional grounds, the three regions representing the incisive, the sectorial, and the grinding parts of the dentition respectively.

Acknowledgements

This work was originally intended as a joint project between Dr L. S. B. Leakey and myself. Although his ill-health in the last years of his life, and his death on October 1st, 1972, prevented Louis Leakey's full participation, a large part of the credit for this work must go to him: credit for his persistence and enthusiasm in initiating the work, for his readiness to accept new interpretations of the fossil material even where these ran counter to his own past work, for the generosity with which he made money available to enable the work to go forward, and, not least,

for his efforts over the years collecting the fossils that made this study possible. For all these things I am deeply grateful.

I would also particularly like to thank Dr Alan Walker in Nairobi, Dr David Pilbeam of Yale, and Drs K. A. Joysey and C. P. Groves in Cambridge for much critical advice and assistance in the earlier stages of this work. In addition, they have commented on various parts of this paper, as have Professor P. V. Tobias and Dr John Harris. I am also grateful to the staffs of the museums that I visited, the American Museum of Natural History, Yale Peabody Museum, the British Museum (Natural History), the Institut de Paléontologie in Paris, the Natural History Museum at Basel, the Kampala Museum, and the National Museums of Kenya. Most of my field work was done in collaboration with Drs John and Judith Van Couvering, who also have contributed a number of significant new primate specimens in the course of their own field work on Rusinga Island. Finally, I should like to thank Dea Andrews for typing and commenting on several of the earlier drafts of this paper.

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Systematic descriptions

Superfamily **HOMINOIDEA** Gray 1825
Family **PONGIDAE** Elliot 1913
Subfamily **DRYOPITHECINAE** Gregory & Hellman 1939

DIAGNOSIS. Oligocene to Pleistocene apes varying in size of comparable parts from animals a little smaller than a gibbon to those somewhat greater than most gorillas.

Dentition. Differs from that of Ponginae in the following features: incisors less stout, relatively higher crowned and more vertically emplaced; canines less robust; often small diastema between upper C and I2, but functional diastema always less than in Ponginae because of vertical emplacement of the Is; usually no diastema between P_3 and C; upper premolars often relatively broader; upper molars more often with lingual cingulum, crown morphology simpler and usually less crenulated; lower molars more often with buccal cingulum, relatively more elongated.

Mandible. No clear-cut and universal features of distinction from pongines but body often much deeper compared to height of teeth; inferior transverse torus sometimes present but with highly variable degree of development; simian shelf not present on any known specimen. The two sides of the mandibular body usually diverge posteriorly more strongly than in Ponginae and the anterior end of the mandible is always much narrower.

Cranium. The one known skull indicates brain size comparable to living apes of similar bulk. No brow-ridges present. No known major cranial features separate this group from Hominidae on the one hand or Ponginae on the other. The floor of the maxillary sinus is less extensive than in Ponginae. (Emended from Simons & Pilbeam 1965 : 118.)

Genus ***PROCONSUL*** Hopwood 1933

DIAGNOSIS. Primitive apes known only from Africa in early to middle Miocene deposits. They range in dental and cranial size from animals smaller than the gibbon to animals approximately the size of female gorillas. Incisors broader and more spatulate and canines less bilaterally compressed than in *Dryopithecus*. The buccal cusp of P^3 is relatively projecting. Upper molars have well-marked occlusal ridges, usually with at least slight development of the protoconule, and upper molar lingual cingula are prominent, unlike *Dryopithecus* and *Sivapithecus*. Cusp projection and wrinkling of occlusal surfaces are greater than in *Dryopithecus* and *Sivapithecus*. Lower molars always with distinct buccal cingula and greater cusp projection than in *Dryopithecus* and *Sivapithecus*. M_3 elongated, with massive development of the hypoconulid. Genial pit of mandible directed more inferiorly than in *Dryopithecus* and *Sivapithecus*, and there is a large symphyseal superior transverse torus and no inferior torus.

TYPE SPECIES. *Proconsul africanus* Hopwood 1933 : 98.

Subgenus *PROCONSUL* Hopwood 1933

DIAGNOSIS. A group of species covering the full size range of the genus. Incisors are broader and lower-crowned than those of subgenus *Rangwapithecus*, the premolars smaller with more projecting cusps, the upper molars relatively broad and the lower molars less elongated. The M^3 is often reduced and the M_3 often narrows distally so that it is triangular in outline. Cingula are absent or small on the premolars. The body of the mandible is slightly more robust than in *Rangwapithecus*, the alveolar processes of the maxilla considerably more robust, and the floor of the maxillar sinus is reduced in extent.

Proconsul (*Proconsul*) *africanus* Hopwood 1933

1932 *Dryopithecus* sp. Keith : 208.
1933 *Xenopithecus koruensis* Hopwood : 97.
1933 *Proconsul africanus* Hopwood : 98.
1950 *Proconsul africanus* Hopwood; Clark & Leakey : 260.
1965 *Dryopithecus* (*Proconsul*) *africanus* (Hopwood) Simons & Pilbeam : 129.

DIAGNOSIS. A species of *Proconsul* intermediate in dental size between the siamang and pygmy chimpanzee. Cingula well developed in maxillary cheek-teeth, particularly mesially and lingually; buccal cusp of P^3 strongly projecting; occlusal ridges and protoconule well developed on the upper molars; M^3 typically much reduced, particularly metacone and hypocone. Total length of upper premolar–molar series less than 40 mm, lower less than 45 mm. Skull lightly built, relatively orthognathous, lacking brow ridges of *Pan* species. Subarcuate fossa for the petrosal lobule of cerebellum present. Post-cranial skeleton with some features characteristic of *Pan*, particularly the development of the deltoid crest and the medial epicondyle of the humerus and the conformation of the distal articular surface of the humerus. (Emended from Simons & Pilbeam 1965 : 129.)

HOLOTYPE. Left maxillary fragment with the crowns of C–M3. BM(NH) M 14084.

LOCALITY AND HORIZON. The Lower Miocene of Koru, Rusinga Island, Mfwangano Island, and Songhor; and the Middle Miocene of Fort Ternan. All the localities are in Kenya.

MATERIAL. 118 specimens which cover the complete dentition and mandible, the maxillary, frontal, and temporal regions of the skull, and much of the postcranial skeleton.

Cranial material. M 32363, frontal and maxillary regions of the cranium and complete mandible; KNM-RU 2036, temporal and occipital regions of the cranium with fragments of maxilla and mandible, and a partial forelimb skeleton. (Pl. 1, p. 93.)

Maxillary material. M 14081 with left M^1–M^2; M 14085 with right M^1; KNM-RU 1705 with left C–M^1; RU 1769, ten associated incisors and canines; RU 1792 with left P^3–M^1; RU 1897 with right C; RU 1904 with left M^1–M^2; RU 1919 with left dp^3–dp^4; RU 1973 with right M^1–M^2; RU 2088 with right M^2–M^3 and associated with left P^4–P^3.

Mandibular material. KNM-RU 1680 with right P_4–M_2; RU 1706 with left P_4–M_3; RU 1728 with left P_4–M_3; RU 1824 with left P_4–M_2; RU 1855 with left M_1–M_3 and right P_4–M_3; RU 1899 with left C; RU 1955 with left P_3–M_2; RU 2093 with roots of left dp_3–dp_4; MW 59 with left C; SO 391 with roots of left M_1–M_3. (Pl. 2, fig. 1, p. 97).

Isolated teeth. M 14085, right M^1; M 14087, right M_3; M 32238, right dp^4; M 32362, left I_1; the remaining specimens are listed in Tables 1–22.

Referred material. Two specimens from Fort Ternan (KNM-FT 16, M^1; and FT 29, P^3) are provisionally referred to this species.

DESCRIPTION. The skull of *P. africanus* has been well described by Clark & Leakey (1951 : 16–28) and in the absence of any new cranial material this description will not be enlarged upon.

Maxilla and premaxilla (Table 1, p. 134–5). The premaxilla is small compared with modern apes. The nasal processes are short and the maxillo-premaxillary suture contacts the nasal aperture about half way up the aperture. The body is small and alveolar prognathism is restricted. The nasospinale–alveolare height is low. The incisor roots are set nearly vertically in the body of the premaxilla and the diastema between C and I^2 is short (up to 3 mm) so that essentially there is no functional diastema in this species, even in males.

The alveolar process of the maxilla is fairly robust. The floor of the maxillary sinus is at about the level of the tips of the molar roots so that the latter do not push up into the floor of the sinus. Specimen RU 2036 is exceptional in having one fairly deeply excavated region of the floor of the sinus above M^1. No specimen is complete enough to measure, but it appears that the sinus is restricted laterally. The tuberosities of the alveolar process vary from short in M 32363, possibly a female, to long in M 14084, possibly a male, but in neither case is it possible to make an accurate measurement. The greater palatine foramen is opposite M^3 in both cases. The zygomatic process of the maxilla is above $M^{1/2}$ in all specimens except the immature maxilla RU 2036, in which it is further forward above M^1. There is considerable variation in the height of the zygomatic process; it is low in RU 2036, but this is to be expected in an immature individual; in the two adult specimens on which it is possible to measure this dimension accurately values of 7·1 mm on a possible female (M 32363) and 10·4 mm on a possible male (M 14084) were obtained. The palate is long and narrow. Clark & Leakey (1951 : 16, 24) estimated palate breadths at M^1 for M 14084 and M 32363 both at 24·0 mm; I agree with the former estimate but have a value of 21·0 mm for the latter. By the time it was adult, RU 2036 would probably have had a palate breadth slightly greater than 21·0 mm.

Mandible (Table 2, p. 136–7). The mandibular symphysis is buttressed by a superior transverse torus. An inferior torus is not developed on any specimen, but the medial surface below the superior torus usually passes vertically downwards and only a little anteriorly. In one case (RU 1728) it passes a little posteriorly so that the most posterior part of the symphysis is near the base. The genial fossa is shallow and has a number of genial pits developed. One specimen (RU 1855) has a mental spine with slight impressions a few millimetres posteriorly on both sides of the body that might mark the insertion of the digastric muscle. Clark & Leakey (1951 : 27, 29) refer to this and to a similar tubercle on M 32363 which they say is for the attachment of the mylohyoid raphe, but the mylohyoid line is very distinct on RU 1855 and it clearly crosses the symphysis at the level of the two inferior genial pits well above the base of the mandible (see Fig. 2).

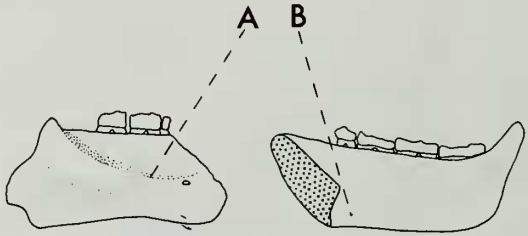


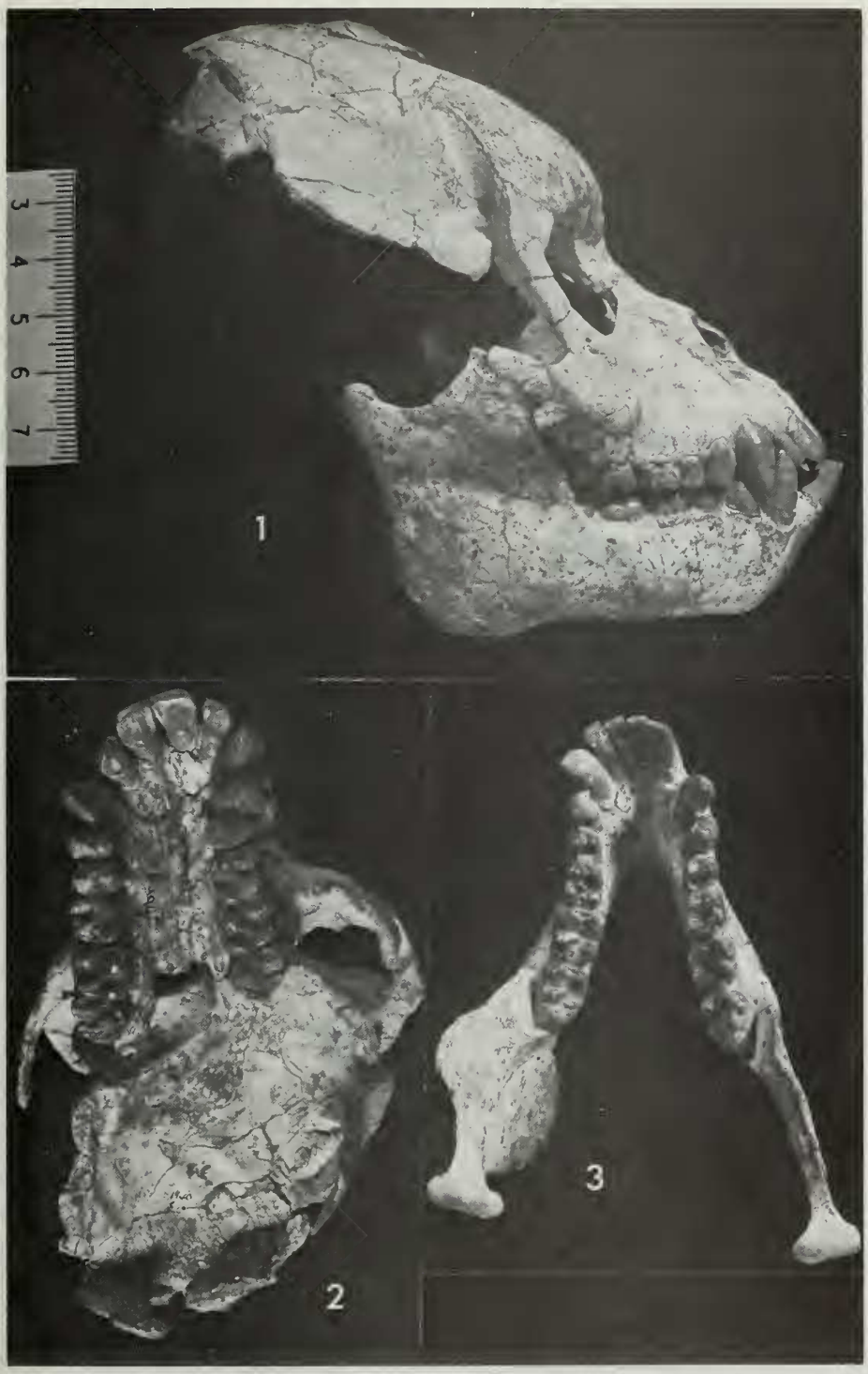
Fig. 2 The mandible of *Proconsul africanus*, × ½. Left, KNM-RU 1680, lateral view; A, line of attachment of buccinator. Right, KNM-RU 1855, medial view; B, position of mylohoid line.

The mandibular body is relatively shallow compared with the symphysis. The mental foramen is situated beneath P_3 just over one third of the way up from the inferior border. Posterior to the mental foramen the buccal surface of the body has a pronounced concavity. In modern apes the buccal cavity follows this concavity, the buccinator muscle attaching along its inferior border, and this appears to be the case here (see Fig. 2). The inferior border is bluntly rounded, thinning out inferiorly posterior to the level of M_3.

The mandibular ramus, by contrast with the body, is very thin. The anterior root overlaps the distal edge of the M_3. The coronoid process is high and pointed, higher than the condyle which follows the usual pongid pattern. Clark & Leakey (1951 : 27) estimate the bicondylar width to be approximately 82 mm. The angle of the mandible is not inflated, and muscle markings on the ramus are indistinct. (See Fig. 4, p. 106.)

Plate 1

Figs 1–3 *Proconsul africanus* (M 32363). Fig. 1, skull and mandible, lateral view. Fig. 2, skull, occlusal view. Fig. 3, mandible, occlusal view.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Upper incisors (Tables 3–4, p. 138–140). The crown of I^1 is relatively broad and spatulate. It is only slightly asymmetrical, and the incisive edge runs nearly the whole width (mediodistal) of the crown. It is usually broader than high, and is also broader than deep. The slimness of the crown is very characteristic, and has been commented on by Clark & Leakey (1951 : 17). The morphology of the crown is simple: an ill-defined basal tubercle is usually present with a swelling running towards the incisive edge. The buccal surface is smoothly convex. Wear is usually confined to the incisive edge, rarely on the lingual surface, and a contact facet develops where the two central incisors meet. In extreme cases lingual wear can pass all the way down the lingual surface to the base of the crown.

The I^2 is smaller and more asymmetrical than I^1. When unworn the crown is usually pointed, the highest point being near the mesial border of the tooth. With wear the tip is flattened so that an incisive edge, directed slightly mesially, is produced. A strongly-developed lingual cingulum is usually present, and running towards the tip of the crown are one or more lingual striations. As on the I^1, wear is usually restricted to the tip of the crown; on one specimen (RU 1964) the distal edge is worn, through contact with the lower canine.

Upper canine (Table 5, p. 141–3). These are short stout teeth, wider than long. The long axis of the canines is only slightly oblique, the angle with the molar–premolar series being about 70°. The most prominent feature is the mesial groove starting from near the tip and increasing in size towards the base, where it ends at the mesial cingulum. The edges of the groove are flattened by wear, the mesial wear facet covering the whole mesial face. The cingulum is well developed and shelf-like. It runs from the buccal border of the mesial groove, at which point there is a distinct tubercle, distally along the lingual margin to the junction of the lingual and distobuccal faces. Wear facets are developed mesially and distally, the former being flat and the latter concave although never cutting deeply into the base of the crown. Frequently there is also a terminal wear facet at the tip of the crown; with increasing wear this usually becomes continuous with the distal facet first and then the mesial facet.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is a bicuspid tooth, varying considerably in the extent to which it is mesiodistally compressed. The buccal cusp is always taller than the lingual one. The crown is greatly elongated buccally so that it has a triangular shape, and the enamel is extended slightly up the buccal root. The mesial ridge of the buccal cusp is very well developed and probably had a shearing action against the distal ridge of the P_3. The distal ridge of the buccal cusp is also well developed, giving this cusp a blade-like appearance. The lingual cusp is rounded and lacks mesiodistal ridges. It has a slight buccal ridge which runs transversely to the buccal cusp in a shallow mesial curve. Distal to the transverse ridge is a relatively large distal fovea the distal part of which is a shelf-like cingulum. There is no lingual cingulum. Mesially, there is a shallow, almost vertically oriented, mesial fovea, which becomes flattened during wear. The cusps are worn initially at the tip, the lingual one much more heavily than the buccal one.

The P^4 is similar to P^3 except that it is not elongated buccally, and the buccal cusp is only slightly higher than the lingual. It is relatively broader buccolingually, the index (bl/md) × 100 being about 10% higher than that of P^3. The mesiodistal ridges of the buccal cusps are well developed. The buccal ridge of the lingual cusp is poorly developed and runs mesially as in P^3. The distal cingulum is strongly developed, as in P^3. Wear, as on P^3, is mainly on the lingual cusp.

Upper molars (Tables 8–10, p. 147–153). M^1 has four equal-sized cusps. The crown is sometimes slightly rhomboidal in shape owing to the extension of the cingulum distally, but the M^1 is the most rectangular of all the upper molars. The trigon is well defined. The mesiobuccal ridge of the protocone runs mesially to the protoconule, situated between the base of the protocone and the mesial edge of the tooth. The protoconule has a well-defined distobuccal ridge going in a buccal direction to the tip of the paracone, and also a short mesiobuccal ridge going to the mesial margin of the tooth, where it contacts the mesial marginal ridge. Between these two ridges is a narrow mesial fovea. The trigon basin is limited distally by the crista obliqua, the distobuccal ridge of the protocone, which runs straight into the lingual ridge of the metacone. The ridges of the metaconule do not appear to be developed at all, and the lingual end of the lingual ridge of the metacone is separated from the metaconule, where it is present, by a sulcus. Completing the trigon, the mesial and distal ridge of the paracone and the mesial ridge of the metacone are well developed,

but the junction of the ridges between the paracone and the metacone is broken by the very deep buccal main groove.

The hypocone is an isolated cusp standing on the lingual cingulum. There is occasionally a slight ridge connecting it to the crista obliqua, but where the metaconule is developed there is no such ridge. The moderately beaded lingual cingulum runs from the mesiobuccal ridge of the protoconule to the mesial border of the hypocone. The large distal cingulum forms most of the distal fovea, and runs from the distal border of the hypocone to the distal border of the metacone. It is slightly beaded, and often has some minor folding. The buccal cingulum, between the paracone and metacone, is very slight and sometimes does not develop at all.

The M^2 is similar to M^1 except that it is larger. The hypocone and distal cingulum are usually extended distally giving a more characteristic rhomboidal pattern to the M^2. The mesial development of the trigon is the same in M^2 as in M^1, but the crista obliqua is usually cut by a longitudinal sulcus. The metaconule has not been observed on any specimens of M^2. The hypocone is large, and has a slight ridge connecting it to the crista obliqua very close to the tip of the protocone. The cingulum is similarly developed to M^1, but is larger all round, especially distally.

The M^3 is greatly reduced in size. Both metacone and hypocone may be lacking so that the distal end of the tooth is abbreviated and has a bluntly pointed triangular appearance. The mesial development of the trigon is the same as in M^1 and M^2 and the protoconule is usually present. The crista obliqua is faintly present, running from the protocone with many breaks to the buccal border of the tooth. There is a slight cuspule there which may represent the metacone. The hypocone is also hard to identify sometimes, for the distal end of the crown has a number of undifferentiated tubercles, and there are several on the crista obliqua itself. The cingulum is massively developed distally and only slightly smaller lingually. It completes the circuit round the tooth without a break.

Lower incisors (Tables 11–12, p. 154–5). The I_1 is high-crowned and symmetrical. The lingual surface is slightly concave and is unmarked by any ridge or cingulum. The buccal surface is gently convex and featureless. Wear is restricted to the tip of the crown along the incisive edge. The I_2 is a more robust and higher-crowned tooth than I_1. The crown is asymmetrical, the distal edge being convex and the mesial edge nearly straight. The highest point of the crown is at the mesial end of the incisive edge, the latter being relatively much shorter than on I_1. The lingual surface of the crown is concave, as on I_1, but it is marked by a slight lingual pillar running nearly to the tip of the crown.

Lower canine (Table 13, p. 156–8). The unworn lower canine has a characteristic morphology, best seen on specimen RU 2036. The mesial ridge of the crown is long and reaches the base of the crown which is only slightly raised to meet it; the distolingual ridge is also prominent, although it ends a little above the base of the crown, and between the two ridges the lingual face of the crown is a strikingly flat triangular surface. It is ended at the base by a discontinuous lingual cingulum. Distal to the distolingual ridge there is another occurrence of cingulum which constitutes an inconspicuous heel of the canine. A variation to this is seen in the 1948 skull (M 32363); the mesial ridge is reduced in length and runs into a more or less continuous lingual cingulum that is elevated mesially to meet it, very like the condition seen in *Limnopithecus legetet*. The cingulum continues distally around the base of the distolingual ridge and forms a more prominent heel than is found in the first type.

The wear patterns reciprocate those of the upper canine. A distal facet is cut distobuccally, on the buccal side of the distolingual ridge, and this wear facet may be extended to the tip of the crown with two regions of maximum wear, one at the base of the crown producing the distal notch and the other towards the tip of the crown. The crown is not heavily worn on any specimen of this species.

Lower premolars (Tables 14–15, p. 159–162). The P_3 is a single cusped tooth, resembling the sectorial type found in gibbons and monkeys but apparently not sectorial in function. The crown is much longer than broad, but is not bilaterally flattened to the extent seen in sectorial premolars. It is set obliquely in the mandibular body, about 60° to the molar–premolar series. The mesial ridge is well developed, running from the tip of the main cusp directly mesially to the end of the lingual cingulum, which is elevated at this point. The distal ridge is also prominent, continuing

the line of the mesial ridge distally to the distal cingulum. There is also a distolingual ridge from the tip of the cusp down to, but not contacting, the lingual cingulum. Distally there is a thickened shelf of cingulum which is bounded buccally by the distal ridge, although it slightly overlaps the end of the ridge to form a short and slight distobuccal cingulum. The cingulum is also well developed lingually, running from the mesial ridge to just below the distolingual ridge.

The P_4 is a bicuspid tooth, characteristically broader than long. The long axis of the tooth is set obliquely, paralleling that of P_3. The two main cusps are aligned buccolingually, with sometimes the buccal cusp slightly mesial to the lingual cusp. They are widely separated and are joined by a moderately well-developed transverse ridge which may be homologous with the distal trigonid ridge of the lower molar. There is a short mesial ridge from the buccal cusp which appears to contact the slight buccal cingulum, and then to continue lingually as either ridge or mesial cingulum to the mesial ridge of the lingual cusp. Enclosed within these ridges is a distinct mesial fovea (perhaps homologous with the trigonid basin). There is a broad and deep distal fovea bounded on either side by distal ridges from the two main cusps. These ridges terminate at the distal angles of the talonid in very slight raised points or tubercles. There is a very slight buccal cingulum, hardly more than a line on the enamel, from the mesial ridge of the external cusp to the distobuccal tubercle. Both tubercle and distal basin appear to be cingular structures. There is no sign of any lingual cingulum.

Lower molars (Tables 16–18, p. 163–170). The lower molars are basically five-cusped and are all longer than broad. They increase in both length and breadth from M_1–M_3, so that M_3 has the largest surface area. The M_1 is smaller and narrower than the others. In cusp size the protoconid, hypoconid and metaconid are about equal. The entoconid is rather smaller, so that the hypoconid has a large area of contact with the metaconid, producing the Y-shaped pattern with respect to the protoconid. Also the entoconid is slightly distal to the hypoconid. The hypoconulid is median. Secondary folds or wrinkles are rarely developed.

In most cases the M_1 is slightly broader distally than mesially. Clark & Leakey (1951 : 19) have described the cusps as 'crystalline', and this best describes their appearance. The edges of the 'crystal' are the ridges, which, with few exceptions, are not discrete ridges at all: they are the lines of contact of two faces of the 'crystalline' cusps. The trigonid ridges are the most strongly developed. The distal trigonid ridge runs without a break from protoconid to metaconid, although it is strongly depressed in the midline of the tooth. The mesial trigonid ridge runs mesially to the mesiobuccal cingulum; it then runs lingually and slightly distally until it meets the mesial ridge of the metaconid, and forms the mesial margin of the trigonid basin and of the whole tooth. This development might at one stage have been cingular, but there is nothing to suggest on any of these specimens that it is so. In addition, there is sometimes a third transverse ridge crossing the floor of the trigonid basin, in effect cutting it into two, and this, like the distal trigonid ridge, runs from the tips of the protoconid to the metaconid. In contrast, the talonid ridges are poorly defined. The talonid basin is fairly deep, but, because the talonid cusps are large, have broad areas of contact with each other and intrude into the talonid, the area of the basin is relatively small. There is a small distal fovea behind the entoconid and hypoconulid. The buccal cingulum is only slightly developed. There is a short section on the mesiobuccal border of the protoconid, but the greatest development is in the interval between protoconid and hypoconid. There is also a further slight development between the hypoconid and the hypoconulid.

Plate 2

Fig. 1 *Proconsul africanus.* Mandible, occlusal view (KNM-RU 2036).

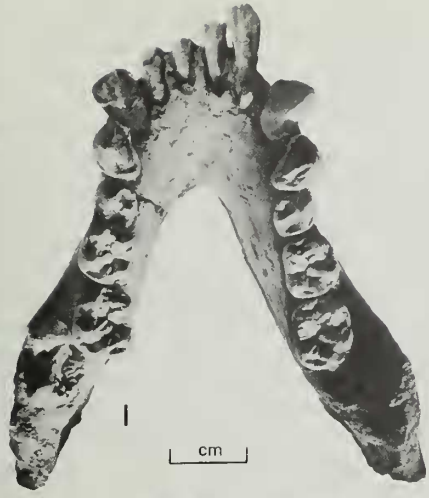
Fig. 2 *Proconsul nyanzae.* Mandible, occlusal view (KNM-RU 2087).

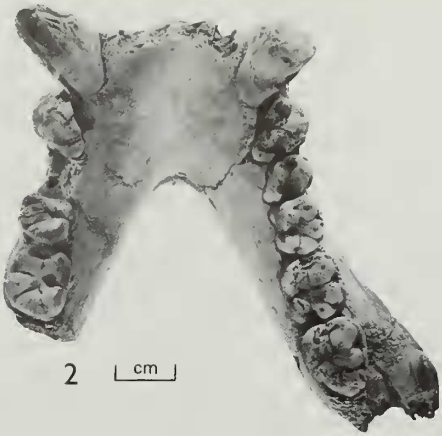
Fig. 3 *Proconsul* (*Rangwapithecus*) *gordoni.* Left mandible, with superimposed mirror image joined along the symphysis, occlusal view (KNM-SO 1112).

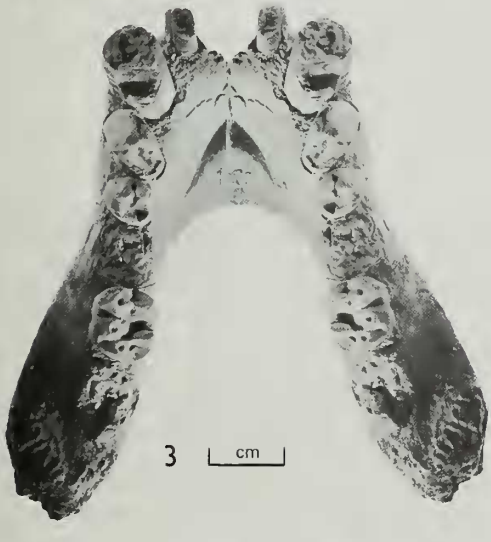
Fig. 4 *Limnopithecus legetet.* Right mandible, with superimposed mirror image joined along the symphysis, occlusal view (KNM-KO 8).

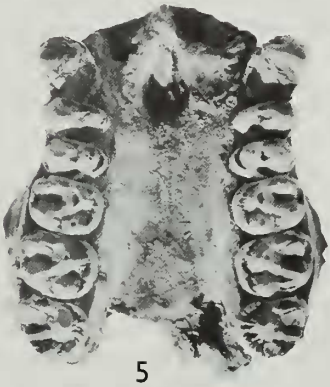
Fig. 5 *Dendropithecus macinnesi.* Palate, occlusal view (KNM-RU 1850).

Fig. 6 *Dendropithecus macinnesi.* Right mandible, with superimposed mirror image joined along the symphysis, occlusal view (KNM-RU 2015).









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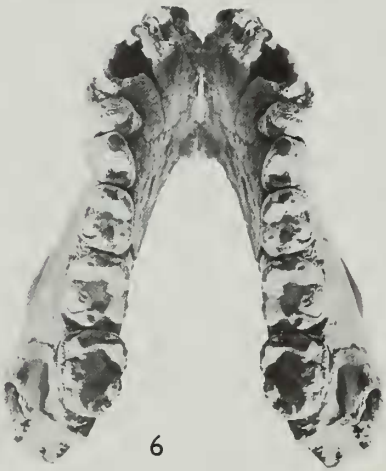


M_2 is longer and broader than M_1. It is essentially similar in morphology but differs in a few details. The trigonid ridges are less well developed although they can still be seen. The distal trigonid ridge is deeply cut by the longitudinal sulcus. The mesial trigonid ridge is still quite well developed and again meets the mesiobuccal cingulum. The trigonid basin is well developed but opens distally into the talonid basin by the deep longitudinal sulcus. The talonid ridges are more strongly defined than on M_1, especially the entoconid–hypoconulid ridge. The talonid basin is clearly circumscribed by the talonid ridges, although the large basal area of the cusps encroach on it. The distal fovea is very clearly demarcated behind the entoconid–hypoconulid ridge and is rather deep and shelf-like. There is some secondary wrinkling of the talonid. The cingulum is variable, but is rather better developed than on M_1 and is found in the same places.

The M_3 is the largest tooth in the lower molar series. It has conspicuous folding and wrinkling of the whole occlusal area. The trigonid ridges are still more poorly defined than in M_2, and the basin, although distinct from the talonid basin, is rather small. The talonid ridges are also poorly defined, and there does not appear to be any entoconid–hypoconulid ridge. The entoconid is reduced, and appears as one of a series of cuspules along the lingual border between the metaconid and hypoconulid. The hypoconulid is a large heel-like cusp, slightly buccally placed. The talonid in the region of the hypoconulid is particularly strongly wrinkled.

Deciduous dentition (Tables 19–21, p. 171–3). The dp^3 is bicuspid with a faint ridge joining the two cusps. It is slightly elongated buccally, and the buccal cusp is slightly higher than the lingual one. The mesial and lingual cingula are small, but there is a massive distal cingulum.

The dp^4 crown morphology is very similar to that of M^1 except in the absence of the protoconule. It is lower crowned than M^1 and is smaller.

A single isolated dc_1 which is an exact replica, on a smaller scale, of the C for instance of KNM-RU 2036, is fairly certainly referred to this species, both for this reason and because of its size.

The roots of dp_3–dp_4 are present on RU 2093, and RU 1865, which probably is a deciduous dp_4, has comparable root measurements. The five cusps are all isolated from one another, with no ridge development. The hypoconulid is small. The protoconid is slightly in advance of the metaconid, and the hypoconid of the entoconid, giving the crown a skewed appearance. The buccal cingulum is poorly developed.

Remarks. *Proconsul* (*Proconsul*) *africanus* is the most distinctive of the species assigned to this subgenus. The main points of difference between it and *P.* (*P.*) *nyanzae* and *P.* (*P.*) *major*, apart from its smaller size, may be summarized as follows. The I^1 is relatively slim buccolingually and broad and spatulate mesiodistally; the Cs are slender-crowned pointed teeth, often with marked asymmetry; the P^3 has a slender and strongly-projecting buccal cusp; the M^2 is the largest molar in the maxillary tooth row, but it does not greatly exceed M^1 in size; the M^3 is strongly reduced, both in size and morphology, and it is often limited to the two mesial trigon cusps; the M_3 is elongated, longer than M_2, but the distal end is abbreviated so that the crown is triangular. These points combine to make *P. africanus* readily distinguishable from the other species of *Proconsul*, although it should be remarked that they do not distinguish it from *Limnopithecus legetet*. The latter, however, has other points by which it may be distinguished, notably its very much smaller size, its elongated P_4s, and its rounded molar cusps which lack the 'crystalline' appearance described for *P. africanus*.

An estimate of the size range of *P. africanus* can be obtained from Figs 7–24, p. 176–191. In most dimensions the top of the range for *P. africanus* just meets the bottom of the range of *P. nyanzae*, but for a few teeth, for example the lower molars, there is some overlap. In cases where there is apparently a large gap between the two species it is more likely because of sample inadequacies than a genuine size difference, as, for example, in the lower canines where it is evident that only the bottom half of the population range is represented (Fig. 19). Greenfield (1972) has suggested that a number of specimens presently assigned to *P. nyanzae* represent these missing male *P. africanus*, and on the evidence of dental size alone this is a possibility. However, in terms of dental morphology and of mandibular or maxillary size and morphology it is more probable that the specimens are correctly placed in *P. nyanzae*, and since the dental size evidence is at best equivocal they will be so treated here.

The distribution of *P. africanus* is limited to western Kenya (Fig. 1). It is most common in the deposits of the Hiwegi Formation of Rusinga Island (Van Couvering & Miller 1969), and it also occurs in similar deposits on the neighbouring Mfwangano Island as well as in the lower deposits there equivalent to the Kiahera Formation of Rusinga (Whitworth 1961). These lower deposits are dated as older than 19·6 ± 0·2 m.y. (Van Couvering & Miller 1969). The youngest record of this species is at Fort Ternan, where the deposits are bracketed by dates of 12·5 and 14 m.y. (Bishop, Miller & Fitch 1969), so that the known time range is at least 5·5 million years. On available evidence the morphology of the species does not seem to change over this time period, but the specimens from the two extremes of the time range are fragmentary and might not show any changes that had occurred.

The distribution pattern just outlined is very similar to that of *Proconsul nyanzae*. This similarity must raise the possibility that the two species ought not to be separated. Their basic similarity in morphology indicates that they had diverged from a common ancestor not long previously to their first occurrence in the fossil record, but in view of the size differences between them it seems unlikely that they are conspecific, unless the combined species was exceedingly variable, and the possibility must be raised that more complete material would show a greater degree of morphological difference between them. Alternatively it is possible that the apparent association of the two species is a artifact of poor collecting techniques, and that they might not be actually associated in single fossiliferous horizons. The little evidence available supports this, in that where one species has been found in recent excavations the other is absent (Andrews & Van Couvering 1975), but sample sizes are small, and this is at best negative evidence for lack of association.

Proconsul* (*Proconsul*) *nyanzae Le Gros Clark & Leakey 1950

1943 *Proconsul africanus* MacInnes : 163.
1950 *Proconsul nyanzae* Clark & Leakey : 261.
1950 *Sivapithecus africanus* Clark & Leakey : 261.
1965 *Dryopithecus* (*Sivapithecus*) *sivalensis* (Lydekker) Simons & Pilbeam : 127.
1965 *Dryopithecus* (*Proconsul*) *nyanzae* (Clark & Leakey) Simons & Pilbeam : 130.
1967 *Kenyapithecus africanus* (Clark & Leakey) Leakey : 157.

Diagnosis. A species of *Proconsul* approximating in dental size to the chimpanzee. Canines well developed and often about as large relative to palate and mandible as in the chimpanzees. Strongly sexually dimorphic, particularly in the canines. Lingual cingulum of upper molars beaded, posterior cingulum well developed. M1 very small relative to M2; M3 slightly smaller than M2 but not reduced morphologically and much bigger than M1. P^3–M^3 length between 40 and 50 mm; P_3–M_3 length 45–55 mm. Maximum depth of mandibular body greater than in *P. africanus* (25 mm), but variable. Symphysis and body relatively gracile. (Emended from Simons & Pilbeam 1965 : 130.)

Holotype. Nearly complete maxilla, but much distorted, with upper dentition except for the incisors. BM(NH) M 16647.

Locality and Horizon. The Lower Miocene of Rusinga Island, Mfwangano Island, and Karungu; and the Middle Miocene of Fort Ternan and Maboko Island. All the localities are in Kenya.

Material. 103 specimens which cover the complete dentition, mandible, maxilla, and parts of the face. Only a few fragments of limb bone can be attributed to this species with any certainty.

Maxillary material. M 16647 palate and maxillary region of face with complete dentition except for the incisors; M 16649 with left P^3–M^1; KNM-RU 1677 complete upper dentition except for the I^2s; RU 1715 with P^4; RU 1718 with P^3–P^4; RU 1803 immature maxilla with I^1, dp^3–dp^4 and M^1, with M^2 unerupted; RU 2031 with broken dp^4 and I^2 unerupted. (Pl. 3, figs 2–3, p. 101.)

Mandibular material. KNM-RU 1674 nearly complete mandible and left maxilla; RU 1676 left tooth row with C–M_3; RU 1678 with P_4–M_2; RU 1679 with P_4–M_1; RU 1710 immature mandible with left P_4–M_2; RU 1711 with P_4–M_1; RU 1716 with unerupted crowns of I_2, C and P_4 exposed; RU 1780 with P_4–M_1; RU 1947 complete mandible and dentition, much distorted;

RU 1982 fragmentary mandible with complete dentition except for the incisors; RU 2087 with left C, P_3 and M_2 and right C–M_2. (Pl. 2, fig. 2, p. 97.)

Isolated teeth. M 32235, right P_3; M 32236, right C; the remaining specimens are listed in Tables 1–22.

Referred material. Six specimens from Fort Ternan (KNM-FT 39 and 28, C; FT 49, I^1 previously assigned to *Kenyapithecus wickeri*; FT 34 and 40, M_3; and FT 2751 distal end of humerus).

DESCRIPTION. This species will be described in conjunction with the next, *P.* (*P.*) *major*.

Proconsul (*Proconsul*) *major* Le Gros Clark & Leakey 1950

1950 *Proconsul major* Clark & Leakey : 261.
1965 *Dryopithecus* (*Proconsul*) *major* (Clark & Leakey) Simons & Pilbeam : 134.

DIAGNOSIS. A species of *Proconsul* with dentition approximately the size of that of the female gorilla. Largest species of *Proconsul*; length of P_3–M_3 may exceed 65 mm. Compared to tooth size, mandibular body much more massive than in *P. nyanzae* and symphysis more massive than in *S. indicus* which otherwise approaches *P. major* in size. M_3 typically larger and longer compared to M_2; much larger than M_1; M^3 larger than M^1, more so than in *P. nyanzae*; the M1 significantly larger than M1 of *P. nyanzae* at 0·02 probability; cingula usually more distinct than in gorilla and simian shelf not developed; crowns of cheek-teeth perceptibly more wrinkled than in *S. indicus*. (Emended from Simons & Pilbeam 1965 : 134.)

HOLOTYPE. Right mandibular body with the crowns of P_4–M_3. BM(NH) M 16648.

LOCALITY AND HORIZON. The Lower Miocene of Songhor and Koru in western Kenya; ? Lower Miocene deposits of Losidok, Moruorot, and Kirimon in northern Kenya; and the Lower Miocene of Napak and ? Middle Miocene of Moroto, Uganda.

MATERIAL. 53 specimens from Kenya which cover parts of the maxilla and most of the upper dentition, all of the mandible and lower dentition except for the I_1 and ascending rami.

Maxillary material. KNM-SO 418 with right P^3–M^1; SO 144 with left P^4; SO 527 with P^3–P^4; SO 529 with right P^3–P^4; SO 542 with right dc, dp^3, dp^4, and M^1, with unerupted crowns of P^3 and P^4, and associated with immature mandible with dp_4 and M_1. (Pl. 4, fig. 3, p. 103.)

Mandibular material. M 14086 with left P_3–M_2 and right P_3–M_2; M 16648 with right P_4–M_3; KNM-SO 396 with right C and left P_4–M_3; SO 404 with left and right mandibular bodies but no teeth; SO 542 see above. (Pl. 4, fig. 4, p. 103; Pl. 5, p. 105.)

Isolated teeth. M 14275, part of molar; M 14297, left I^1; M 14331A, right P^3; M 14331B, left M^3; M 32228, right dc; M 32237, right M_3; the remaining specimens are listed in Tables 1–22, pp. 134–174.

Referred material. One specimen from Moruorot, two from Losidok, and one from Kirimon, all in northern Kenya (MO 26, right mandible with dp_4 and M_1, with I_2 and C in alveolus; LS 7, left maxilla with M^2–M^3; LS 8, left C and Kirimon, C.).

Five specimens from Moroto and 19 from Napak in Uganda have been described by Allbrook & Bishop (1963) and Pilbeam (1969). The material is as follows.

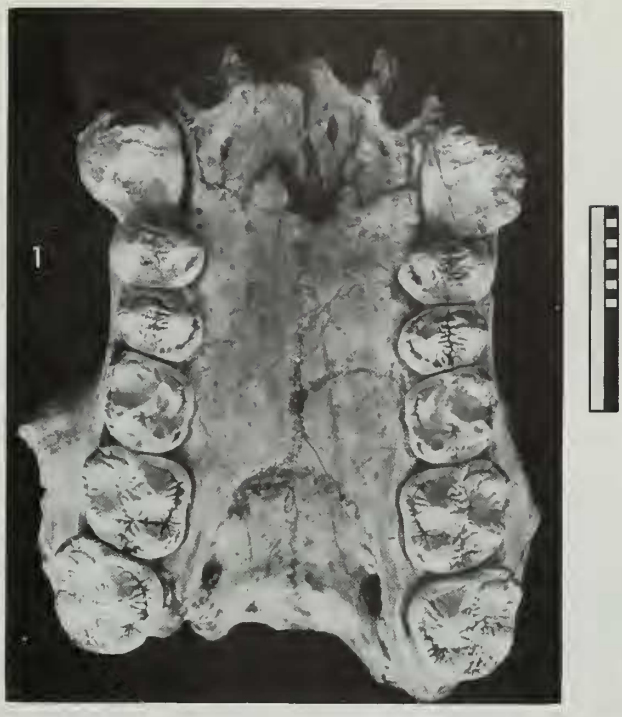
Napak I UM-P 62-03, right C; 62-09, left M^2; 62-13, immature mandible with M_1; 62-14, right M_2; 62-15, left M_2; 62-16 mandible with left P_4–M_1. Napak IV UM-P 64-01, right M^1; 66-41, right M^1; 68-04, P_3. Napak V UM-P 62-04, right C; 62-05, left C; 62-06, mandible with P_4; 62-07, right M^1; 62-08, left M^2; 66-02, right P_4; 66-03, right I^2; 66-20, C ?; 69-01, right P_4; 69-02, right M^1.

Moroto I UM-P 67-36, C. Moroto II UM-P 62-10, mandible with right M_1; 61-11, palate with complete dentition except for tip of right C and lingual half of left P^3; 62-12, left C; 66-01, mandible fragment.

Plate 3

Fig. 1 *Proconsul* (*Rangwapithecus*) *gordoni*. Palate, occlusal view (KNM-SO 700).

Figs 2–3 *Proconsul nyanzae*. Left maxilla with P^3–M^1 (M 16649). Fig. 1, lingual view. Fig. 2, occlusal view.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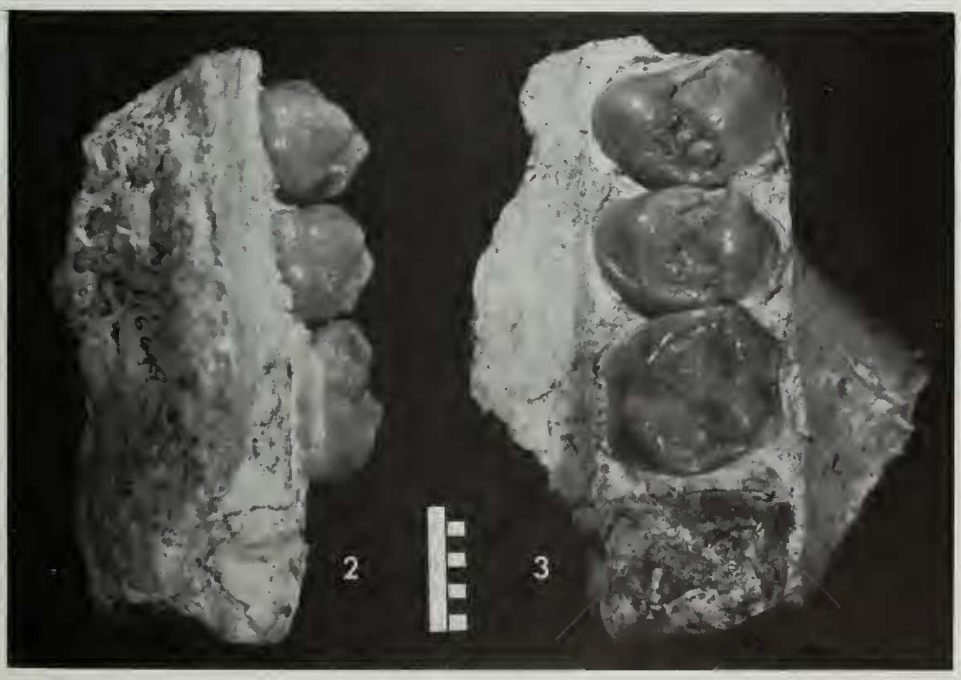
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DESCRIPTION. These two species, *P. major* and *P. nyanzae*, are here assigned a single morphological description. They are almost identical morphologically, but differ in size and distribution. Differences, where they occur, are mentioned in the text.

Maxilla and premaxilla (Table 1, p. 134–5). The premaxilla was evidently a substantial-sized bone forming most or all of the lateral walls of the nasal aperture. MacInnes (1943 : 164) stated that the base of the nasal aperture lies only just above the alveolus, but although the distance is not nearly as great as in modern pongids, the naso-alv. ht varies from 13 to 16 mm, indicating a robust bone. The comparable value in *P. major* is 16·7 mm, and the index (naso-alv. ht/nasal ht) $\times 100$ is 18%. The anterior surface of the bone on UM-P 62-11 is swollen in the region of the left central incisor root and heavy wear on this tooth attests to its being well used. There is a considerable diastema (5–7 mm) between the canine and lateral incisor, and this is greatly increased in effect by the procumbency of the incisors which results in a large functional diastema. Nasal height can be estimated for both species, 72 mm in *P. nyanzae* and 98·5 mm in *P. major*. This is similar to values seen in female and male gorillas respectively. However, the nasal aperture is much narrower than in the gorilla, although relatively wider in *P. major* than in *P. nyanzae*: see Table 1. The floor of the nasal aperture is a simple gutter and is angled sharply with the alveolar border of the premaxilla. No nasal spine is visible.

The alveolar process of the maxilla varies from being exceedingly robust in the region of the canine juga to relatively shallow posteriorly. The canine juga are strongly developed so that there are slight concavities anterior (above I^2) and posterior (above P^4) to it. The floor of the maxillary sinus runs from the distal edge of P^4 into the tuberosities of the alveolar process and on into the pterygoid plate. The floor of the sinus is slightly excavated between the roots of the molars but it cannot be said to be divided into separate loculi. The tuberosities project 7–9 mm beyond the distal end of M^3 and are inflated. The greater palatine foramen is opposite M^3. The zygomatic process of the maxilla is set above M^2 in most cases. This is the usual pongid condition. The height of the process is 12–17 mm with the greatest heights in the probably male specimens. The palate is long and narrow and very gorilla-like. The incisor alveolus projects anteriorly to the canines, and the maxillopalatine suture is set relatively far posteriorly (opposite M^3) so that the palate is lengthened both anteriorly and posteriorly. In *P. major* the palate narrows posteriorly, the widest point being between the canines, but in *P. nyanzae* the tooth rows apparently diverge slightly posteriorly. M 16647 is the only intact palate in the latter species, but the posterior distortion makes it impossible to be sure of the actual degree of divergence.

Mandible (Table 2, p. 136–7). The mandibular symphysis is variable both in extent and degree of buttressing. On most specimens of *P. nyanzae* it is deep and fairly gracile but on some of the *P. major* specimens it is more robust. All have a superior transverse torus, and it is the greater development of this that makes the symphysis more robust in *P. major*. The internal surface of the symphysis consists of a long flat slope running posteriorly from the incisor alveolus to the most posterior point of the superior transverse torus, which usually reaches to the level of P_3. At its greatest development, in *P. major*, the superior transverse torus occasionally reaches the level of the mesial quarter of P_4. Below the torus the symphyseal plane runs anteriorly, and is hollowed out slightly in the region of the genial fossa. On specimen RU 1840, which Leakey

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Plate 4

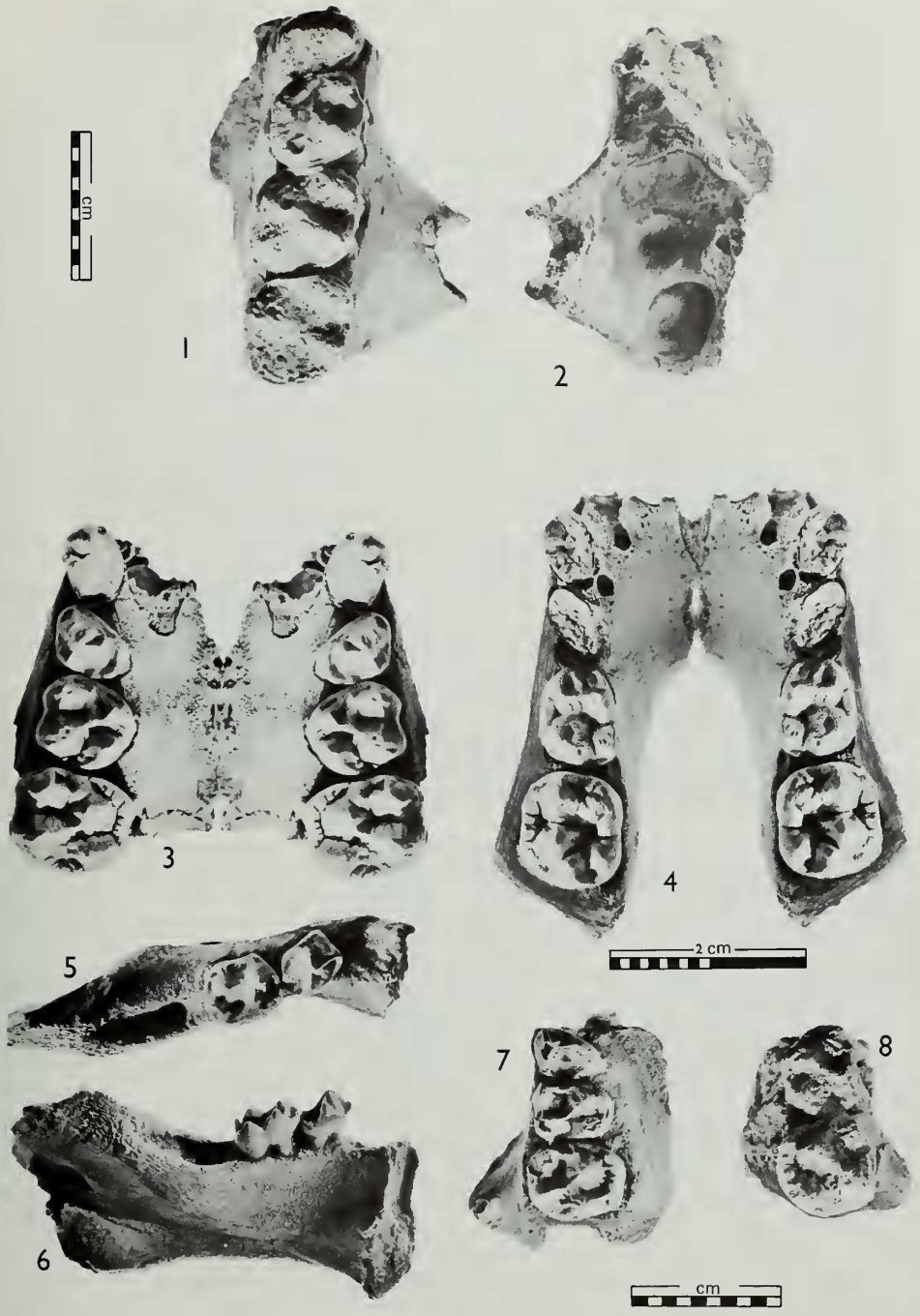
Figs 1–2 *Proconsul* (*Rangwapithecus*) *vancouveringi*. Left maxilla with P^4–M^3 (KNM-RU 2058). Fig. 1, occlusal view. Fig. 2, superior view.

Figs 3–4 *Proconsul major* (KNM-SO 542). Fig. 3, right maxilla with dc-dp^4 and M^1, with superimposed mirror image joined along the palatal suture, occlusal view. Fig. 4, right mandible with roots of dc–dp_3, crowns of dp_4 and M_1, with superimposed mirror image joined along the symphysis, occlusal view.

Figs 5–6 *Limnopithecus legetet*. Left mandible with dp_3–dp_4 (KNM-SO 1073). Fig. 5, occlusal view. Fig. 6, lingual view.

Fig. 7 *Limnopithecus legetet*. Right maxilla with dp^3–dp^4 and M^1, occlusal view (KNM-SO 536).

Fig. 8 *Proconsul* (*Rangwapithecus*) *vancouveringi*. Left maxilla with dp^4 and M^1, occlusal view (KNM-RU 1778).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(1967) assigned to '*Kenyapithecus africanus*' on the basis of the supposed presence of a chin, the genial fossa is directed almost directly downwards on his reconstruction. When the fossa is directed posteriorly, so that the tongue muscles can attach, the 'chin' disappears. This is shown diagrammatically in Fig. 3. The genial fossa has one or two paired pits, probably marking the attachment of the genioglossus and geniohyoid muscles. The mylohyoid muscle seems to have been attached along the lower lip of the genial fossa, as the mylohyoid line runs directly below the pits and the fossa. A prominent spine is present on specimen SO 396 with clear digastric impressions on either side of it. The digastric fossa and spine extends several millimetres up from the base of the mandible.

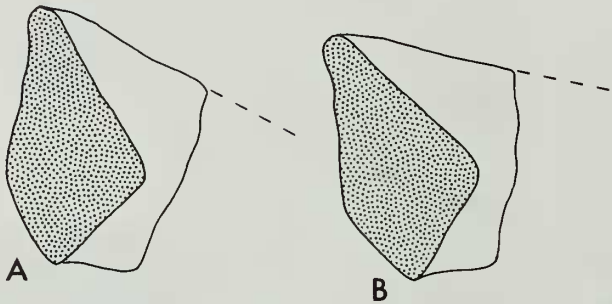

Fig. 3 KNM-RU 1840 '*Kenyapithecus africanus*' mandible, × 1. A, cross-section of the symphysis in the orientation of Leakey (1967 : fig. 5e) with the genial fossa opening downwards and the tooth row sloping downwards. B, alternative orientation showing tooth rows level and genial fossa opening posteriorly. The 'chin' is much less obvious in the second orientation.

The mandibular body varies in the same way as the symphysis. The largest specimens of *P. nyanzae* have body depths as deep as or deeper than *P. major*, but they are more gracile. The mental foramen is single and situated beneath P_3/P_4. The concavity for the buccal cavity is pronounced and in some cases seems to extend surprisingly far towards the base of the mandible. It always extends down to the level of the mental foramen, which is just over one third of the way up from the inferior border of the mandible. The inferior border is bluntly rounded.

The mandibular ramus is preserved in a broken state on specimen RU 1674. It has been described in detail by MacInnes (1943) and Clark & Leakey (1951 : 46–47). It is high and very large relative to the size of the body of the mandible, and has a pronounced posterior slope. A remarkable feature of this specimen is the posterior divergence of the mandible which leads to the bicondylar width of 112 mm. This is similar to values in male chimpanzees. (See Fig. 4.)

Upper incisors (Tables 3–4, p. 138–140). The I^1 is very high-crowned. The mesiodistal length is greater than the buccolingual length but is less than the height. The lingual surface of the tooth is moderately concave and has a broad stout median pillar running half way to the tip of the crown, and composed of a number of ridges that originate from the prominent lingual cingulum. Wear is usually confined to the incisive edge, and in one case only (MB 104) does it extend several millimetres along the lingual surface of the tooth. There are slight differences in shape and morphology accommodated within this sample, but they are not large enough to denote a specific difference.

The I^2 is high-crowned and caniniform. The crown is triangular in shape and only slightly oblique, as the mesial ridge is almost as long as the distal one. There is a small median pillar,

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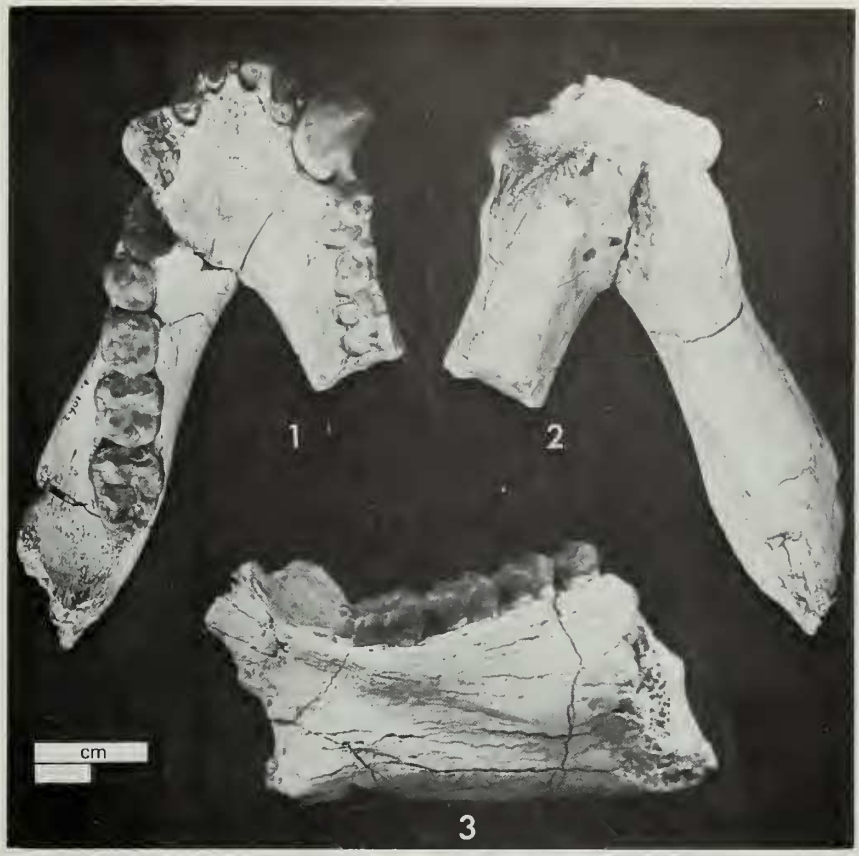
Plate 5

Figs 1–3 *Proconsul major*. Mandible with right C and left P_4–M_3 (KNM-SO 396). Fig. 1, occlusal view. Fig. 2, inferior view. Fig. 3, left mandibular body, lingual view.

Fig. 4 *Proconsul major*. Left I^1, lingual view (M 14297).

Fig. 5 *Proconsul major*. Left M_3, occlusal view (M 32237).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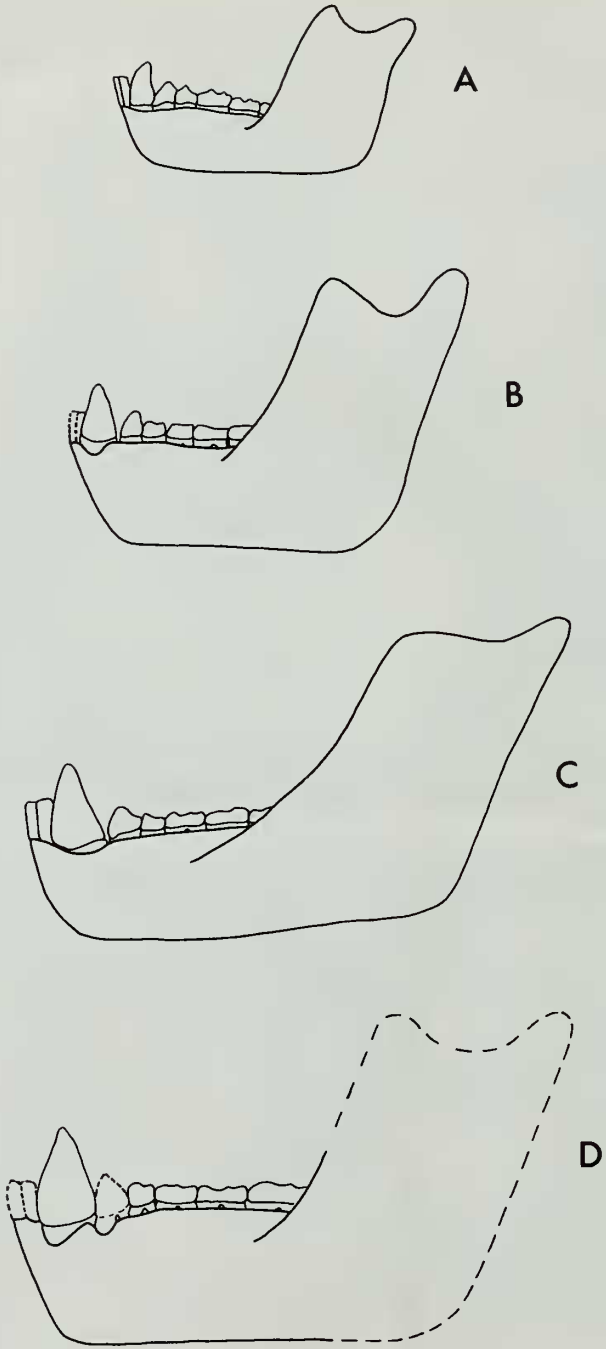


Fig. 4 Mandibular size variation in *Proconsul*, × ⅓. Lateral views of: A, *P. africanus*. B, *P. nyanzae* female. C, *P. nyanzae* male. D, *P. major* male.

consisting, as in I^1, of numerous ridges or striations, but the lingual cingulum is more prominent than in I^1. Distally the cingulum forms a slight heel. With the onset of wear the shape of the tooth alters completely. The tip of the crown is quickly worn flat, and the incisive edge thus produced is concentrated on the mesial side of the tip of the worn incisor. A relatively large mesial contact facet is formed against I^1, and a very deep wear notch is cut into the distal edge of the crown by the lower C.

Upper canine (Table 5, p. 141–3). These are large tusk-like teeth with rounded crown outlines. The crown is moderately bilaterally compressed, and the long axis of the tooth is in line with the molar–premolar tooth row. The crown has a shallow mesial groove running into the lingual cingulum at its mesial edge; the lingual face of the crown is furrowed by grooves and ridges as far as the distal ridge and the lingual cingulum is continuous as far as the distal ridge. Mesial and distal wear facets are developed, the former being a flat facet extending across the mesial groove, and the latter being a deeply-cut concave facet cutting across the distal ridge and quickly obliterating it.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is bicuspid, broader than long, and buccally elongated to give its typical triangular shape. The buccal cusp is higher than the lingual one but less so than in *P. africanus*. There is no ridge development on the occlusal face but there may be secondary wrinkling. Both mesial and distal cingula are prominently developed, and where they meet the mesial and distal ridges of the buccal cusp small tubercles may be developed. There is no lingual cingulum. Wear occurs on both cusps, but the lingual one is worn down more quickly than the buccal one, the latter having the faceting restricted to its lingual face.

The P^4 is similar to the P^3 but tends to have a slightly higher breadth/length index. It is usually smaller than P^3. The lingual cusp is nearly as tall as the buccal one and there is no buccal elongation of the crown. A transverse ridge joining the two cusps is occasionally present but usually the occlusal surface is broken up by secondary wrinkling as in P^3. The mesial cingulum is smaller and the distal cingulum much larger than in P^3.

Upper molars (Tables 8–10, p. 147–153). The M^1 is the smallest molar, and in *P. nyanzae* it is conspicuously smaller than M^2. It has a squarely built crown with all four cusps approximately equal. The cusps are large and occupy most of the occlusal area, resulting in a relatively constricted trigon basin and mesial fovea. The trigon ridges are moderately well developed, and are similar to *P. africanus* in most respects. The talon region of the M^1 is restricted. The hypocone is present as an isolated cusp separated from the protocone by a well-defined sulcus. There is no distal fovea. The cingulum is moderately large. The lingual cingulum runs continuously without a break from the mesial branch of the mesiobuccal ridge of the protocone to a small distal ridge from the hypocone. The cingulum sometimes present on the hypocone is presumably a secondary structure, arising later than the lingual cingulum of the protocone and the hypocone itself, but the two are now continuous. There is also a large distal cingulum running between the distal ridges of the hypocone and the metacone. The buccal cingulum is a small shelf at the base of the buccal main groove in the interval between the paracone and the metacone.

Wear exposes the dentine at the tips of the cusps, on the lingual side initially and much later on the buccal side. There is a fairly steep wear gradient in *P. nyanzae*, in which the dentine may be exposed over the whole lingual surface of M^1 while only just appearing at the tips of the lingual cusps of M^2 and M^3. In *P. major* the wear gradient is less steep.

The M^2 is much larger than M^1 and the ridges are less well defined and the cingulum much larger. There is a small protoconule at the end of the mesiobuccal ridge of the protocone, but the buccal ridges of this cusp are poorly defined. The crista obliqua is low but well defined. It is cut slightly by the distal branch of the longitudinal groove. Where this joins the distinct lingual groove between hypocone and protocone a small distal fovea is produced. The lingual cingulum is very prominent, especially on the protocone, and is moderately strongly beaded. On the hypocone and distally between the hypocone and metacone the cingulum is very large.

The M^3 is smaller than M^2 but it is still a well-developed tooth. This contrasts with *P. africanus* in which the M^3 is much more reduced. The distal cusps are generally slightly reduced in size but are still prominent, and the tooth outline is still predominantly square. The occlusal surface has poorly-defined mesial ridges, although the protoconule is faintly present. The trigon appears

very greatly expanded, as there is no mesial fovea, so that it extends mesially all the way to the mesial marginal ridge. The crista obliqua is low and segmented, cut by sulci. The lingual cingulum is smaller than on M^2 and is strongly beaded, breaking at the hypocone and continuing distally as a very large distal cingulum. There is considerable secondary wrinkling over the occlusal surface as a whole.

Lower incisors (Tables 11–12, p. 154–5). The lower incisors are small relative to canine size. The I_1 is a slim high-crowned tooth, wider buccolingually than mesiodistally. All the specimens are heavily worn so little crown morphology can be seen; RU 2030 is the best preserved and is unusual in being much wider mesiodistally than RU 1947 and in having a marked concave curvature of its lingual surface. It resembles a chimpanzee I_1 while the other specimens are more like the gorilla I_1. In addition the other isolated incisors have a surprising amount of lingual wear, sometimes extending beyond the base of the crown, but the two Rusinga specimens have terminal edge wear only. While provisionally referring these specimens to *P. nyanzae*, the heterogeneity of the sample must be noted; even the two Rusinga specimens, one of which is part of a complete dentition clearly representative of *P. nyanzae* (RU 1947), differ greatly from each other.

On specimen RU 1947, where both lower incisors are preserved, I_2 is much larger than I_1. In particular, it is very much thicker buccolingually. It is similar to I_1 in morphology except for the slight mesial skewing of the crown, the distal edge of the crown being slightly convex and the mesial edge nearly straight.

Lower canine (Table 13, p. 156–8). The canine is a large tusk-like tooth on all specimens. This applies even to RU 1674 which is smaller than the others in most other dimensions. The canine is set strongly obliquely to the line of the molar–premolar tooth row. In cross-sectional outline it has a flattened face mesiolingually and a rounded border curving evenly round 270° distobuccally to mesiobuccally. The mesial ridge runs directly mesially, that is down the face of the crown closest to the lateral incisors. It meets the lingual cingulum at a slight elevation, and although the extent of this seems to vary considerably, it is rarely as well developed, and the mesial ridge as shortened, as in *P. africanus*. There is a slight groove immediately lingual to the mesial ridge. There is also a ridge which runs distolingually, but it always ends imperceptibly before it reaches the cingulum. The lingual cingulum is moderately well defined. It is strongest mesially, tapering off distally, and it ends fairly abruptly at the distobuccal angle. Wear occurs distally, starting near the tip and working downwards. This distal facet is usually flattish, and even with heavy wear does not become concave and does not cut deeply into the crown. Wear is only occasionally seen on and across the tip of the crown.

Lower premolars (Tables 14–15, p. 159–162). The P_3 is a one-cusped but only moderately sectorial type of tooth. It is elongated, and set obliquely across the line of the molar–premolar series, but the frequent presence of a beak-like process mesially makes the tooth appear less oblique and more mesiodistally aligned, although the roots are always set strongly obliquely. The beak-like process is the result of the fusion of the mesial ridge and the mesiolingual cingulum, both of which are prominent. The prominent mesiolingual cingulum ends at its junction with a varyingly developed lingual pillar, and distally there is a smaller distolingual cingulum not continuous with the mesial part. The lingual surface between the mesial and lingual ridges is typically flat and has a triangular outline. The distal ridge is well defined, running to the distobuccal angle.

The P_4 is bicuspid with the buccal cusp considerably larger than the lingual one. The cusps are set transversely to the general tooth row, but the long axis of the tooth is oblique. The talonid projects distolingually, and the trigonid mesiobuccally, so that the tooth is elongated in these directions. This gives the skewed appearance to the tooth already described for *P. africanus*, and in most other respects also the P_4 is identical to that of *P. africanus*.

Lower molars (Tables 16–18, p. 163–170). The M_1 is smaller than M_2 in both species, but the difference is much greater in *P. nyanzae* than in *P. major*. The mean indices for $(M_2/M_1) \times 100$ are 116% for *P. major* and 124% for *P. nyanzae*. The M_1 is slightly broader distally than mesially. It has five equal cusps, the hypoconulid being fully developed and set slightly buccal to the midline. The cusps appear less 'crystalline' than in *P. africanus*, and are more swollen and bulbous.

The occlusal ridges are correspondingly less well developed. The distal trigonid ridge is deeply depressed in the midline of the tooth and is slightly cut by the longitudinal sulcus, but it is considerably higher than the talonid floor even at its lowest point. The talonid ridges are poorly defined with the exception of the entoconid–hypoconulid ridge. The hypoconid in particular is isolated. The buccal margin of the tooth is formed by the buccal cingulum, and is indented between the buccal cusps. The invaginations are continued into the talonid by grooves, and it is both these factors that give rise to the isolation of the hypoconid. Wear follows the usual pongid pattern, the buccal cusps being worn down and dentine exposed first. Wear is often much heavier in *P. nyanzae* specimens than in *P. major*, and the former species has a steeper wear gradient as described for the M^1.

The M_2 is a much larger tooth than M_1. It is slightly more broad compared to its length. The trigonid and talonid basins are more strongly differentiated by ridges. The trigonid basin is flat and shallow; this is emphasized by the mesial wear pattern of M_2, the hypocone of M^1 being restricted mesially by the medial position of the hypoconulid of the M_1, so that it occludes entirely on the trigonid basin of M_2. The talonid basin is very large, and is completely enclosed by cusps and ridges. The hypoconulid is buccal to the midline. The cingulum is more strongly developed than in M_1, with the consistent occurrence of a small mesiobuccal cingulum on the protoconid and in the interval between the buccal cusps.

The M_3 is bigger than M_2 in all cases, but the size ratio varies considerably. In general, the larger the overall size of the tooth row, the greater the difference in length between M_2 and M_3. The M_3 narrows distally in *P. major*, and has a triangular outline as in *P. africanus*. The entoconid is reduced and is set far back from the metaconid, and the hypoconulid, while not as tall as on the other cusps, is spread out more and occupies a greater surface area of the occlusal surface. In *P. nyanzae* the M_3 is not reduced distally and is a large elongated rectangular tooth.

Deciduous dentition (Tables 19–21, p. 171–3). The upper dc is a small, low-crowned tooth, morphologically rather featureless. There is no mesial groove or ridge formation. The lingual cingulum is massive, and is continuous along the lingual border. There is no diastema between dc and di_2. The long axis of the crown is set in line with the line of the molar–premolar tooth row.

On the dp^3 there are two main cusps. The buccal cusp is higher and much bigger than the lingual one, and the buccal side of the crown is greatly elongated mesiodistally. No ridge development was observed on the relatively worn specimens. The mesial cingulum is well developed mesiobuccally, and the distal cingulum is very well developed, forming a shelf across the distal end of the tooth. The buccal terminations of both cingula are marked by low elevations or tubercles.

The dp^4 is a typically molariform tooth, very similar to M^1. The four cusps are equal, and the ridges connecting them are not strongly developed. The lingual cingulum is less shelf-like than in M^1 but the lingual edge of the tooth is swollen lingually suggesting progressive cingulum development (or loss). The protoconule does not appear to be developed on any specimens.

No crown of the lower dc is known. Measurements of the root of four specimens indicate that it would probably be a small tooth, and there may be some specimens in the collection incorrectly identified as permanent C of a smaller species.

Only one crown of the dp_3 is known, and that an isolated one, so the identification is uncertain. SO 589 is clearly a deciduous tooth judged on its thin enamel, splayed roots, and low crown; it is the same order of size as the root impressions on the immature mandibles, so it is very likely that it belongs to *P. major*. The mesial and distal ridges are poorly developed. The lingual ridge is more distinct, but there is no tubercle or second cusp present where it meets the lingual cingulum. The cingulum is massive, but is present as a swelling lingually rather than as a shelf. The talonid basin is rather shallow and poorly defined.

The dp_4 is a typically molariform tooth very like M_1. It is lower-crowned and lower-cusped than M_1, the hypoconulid is smaller, the buccal cingulum is much less well developed, and the tooth is more elongated. Also the talonid breadth exceeds the trigonid breadth more than in M_1. The cusps are set well in from the margins of the tooth so that the occlusal surface is restricted. A striking feature of this tooth is the elongated trigonid region mesial to the metaconid. This arises partly because the protoconid is set far mesial to the metaconid, and partly because the trigonid basin is relatively very extensive. The isolated tooth recorded as of *P. major* from Rusinga

Island is the largest of the specimens and as such has been retained in *P. major* even though it is the only specimen of this species now known from this site (RU 1767).

REMARKS. The main difference between *P. nyanzae* and *P. major* is one of size, but that this is not a consistent difference can be seen by reference to the tables of measurement (Tables 1–21). Nearly all the teeth could just be encompassed within the range of a single species with slightly greater than gorilla-type sexual dimorphism, but this assumes, naturally, that the large specimens are male and the small female. The distribution of this hypothetical species is not so easily explained, however, for the large specimens are all found at Songhor and Napak, while the small ones come from these two sites and Rusinga Island. It is most unlikely that in the good Rusinga sample no males have been found, so it must be assumed that the size difference in this instance cannot be attributed to sexual dimorphism, but must be owing to some level of taxonomic difference.

Part of this problem centres on whether there is any *P. nyanzae* at Songhor or not. Clark & Leakey (1951) assigned specimens from Songhor to this taxon, but Pilbeam (1969 : 71) reassigned some of the Songhor mandibular specimens as small *P. major*. The maxillary specimens had already been reassigned by Leakey to his taxon '*Kenyapithecus africanus*'. At this stage, therefore, there was a complex situation: large maxillary specimens only were put in *P. major* and these were clearly not representative of its full range of variation; all large and small mandibular specimens from Songhor were put in *P. major*, representing a more plausible range of variation for a species of this size; maxillary specimens only (from Songhor) were still in '*K. africanus*', and some odd fragments of *P. nyanzae* were left over. Accepting Pilbeam's reassignment of mandibular specimens, it seems most reasonable to follow suit with the maxillary specimens and refer all the Songhor pongids of this size to the one taxon *P. major*. This is the position adopted here. Apart from Songhor there remains one specimen probably belonging to *P. major* from Rusinga Island. This is specimen KNM-RU 1767, a lower deciduous molar. (The clavicle fragment from Rusinga Island mentioned by Clark & Leakey (1951 : 98) is a fragment of a crocodile limb bone.) The deciduous molars can be identified with more certainty now as *P. major* because the same tooth is preserved together with the first permanent molar on the mandible SO 541 which clearly belongs to this taxon.

In addition to the size differences there are a number of morphological differences that will be summarized briefly here. On the maxilla the nasal aperture is relatively broader in *P. major* than in *P. nyanzae*, the palate is relatively longer and narrower, the tooth rows converge posteriorly while in *P. nyanzae* they diverge, and the floor of the maxillary sinus is simple in *P. major* and more complex in *P. nyanzae*. On the mandible the main difference is the degree of robusticity, both the symphysis and body of the mandible of *P. major* being considerably more robust than those of *P. nyanzae*. This is emphasized by the nature of the sexual dimorphism of both; the larger males of *P. nyanzae* have mandibles nearly as deep as those of male *P. major* but more gracile and the small females of *P. major* have mandibles as shallow as those of female *P. nyanzae* but more robust. In the dentition there are also a number of differences, but also some striking similarities. The incisors and canines are morphologically identical, and when the canine lengths are plotted in a frequency diagram for both taxa together a bimodal distribution is obtained (but with 'males' at Songhor and 'females' at Rusinga as already discussed). In the premolars, the lower premolars are more bilaterally compressed in *P. nyanzae* than in *P. major*, but the uppers are similar. The first molar, especially the lower, is characterized by its small size relative to M2 in *P. nyanzae*. However, the difference is not all that great between it and *P. major*, which also has a relatively small first molar. The M_3 is relatively more elongated in *D. major* and the distal cusps are characteristically atrophied, while in *P. nyanzae* it is a broad rectangular tooth not reduced at all. Similarly the M^3 is relatively large in *P. nyanzae* and reduced in *P. major*.

There were thus two populations of large pongids in the Kenya Miocene, one centred on the southern sites around the Rangwa volcano (Rusinga and Mfwangano Islands and Karungu) and the other on the northern sites around the Tinderet volcano (Songhor and Koru) and Napak and Moroto. Whether these were subspecies belonging to one highly variable species, or separate but obviously closely related species, it is not possible to tell on the available dental evidence.

Hopefully when more postcranial bones are known a definite answer may be forthcoming. In the meantime, on the basis of the differences between them, the two species will be retained.

Brief comment might be made here of Leakey's (1967) taxon *Kenyapithecus africanus*. There is no justification for retaining this species, and as discussed above the specimens assigned to it have been variously reassigned to *Proconsul nyanzae* and *P. major*. For most of the specimens this course needs no justification, but some explanation is considered necessary for the reassignment of specimen M 16649 to *P. nyanzae*. This was described by Clark & Leakey (1951 : 63) as the type specimen of *Sivapithecus africanus*, mainly on the grounds of the near-absence of molar cingula, and, hence, similarity with the Asian dryopithecines then assigned to the genus *Sivapithecus*. This similarity was accepted by Simons & Pilbeam (1965 : 127) who actually included it in the hypodigm of one of their Asian species, *Dryopithecus* (*Sivapithecus*) *sivalensis*. Leakey (1967 : 157) subsequently removed it from the Dryopithecinae by describing it as a species of *Kenyapithecus*, ancestral to *K. wickeri* from Fort Ternan. Finally, Pilbeam (1969 : 115–123) discussed the whole problem in great detail, and concluded that most of the '*K. africanus*' specimens had best be described as *Dryopithecus* sp. indet., that phylogenetic relationship with *Ramapithecus* species (including '*Kenyapithecus*' *wickeri*) was improbable, and that the most likely relationship was with *D.* (*S.*) *sivalensis*. I agree with Pilbeam on nearly all of his conclusions, including his phylogenetic ones, but I do not see any reason for separating these specimens from their contemporaries in Kenya by referring them to an unknown species of *Dryopithecus*. The crown morphology of the molars and premolars is very similar to that of *P. nyanzae*: both P^4 and M^1 have small lingual cingula; the protocone and protoconule development of M^1 is identical to that of *D. nyanzae*; the M^1 is extremely small relative to the premolars and also, judged on the roots, to M^2; the canine root is very large, indicating a large crown; there is a posterior canine fossa associated with the large canine root; and the height and position of the zygomatic process are within the known range of variation of *P. nyanzae*. The main differences from *P. nyanzae* are that the tooth crowns are less crenulated, the cingula, though present, are smaller, and the M^1 is extremely small relative to the other teeth. I think the similarities outweigh the differences and that most of the '*K. africanus*' specimens, including M 16649, belong with *P. nyanzae*, which could well be ancestral to the later-occurring *S. sivalensis*.

Subgenus *RANGWAPITHECUS* Andrews 1974

Diagnosis. A group of species approximating in size to the gibbon and siamang. Incisors high-crowned and relatively very narrow compared with subgenus *Proconsul* s. str. Upper molars and premolars elongated, the molars usually longer (mesiodistally) than broad, low-cusped and the occlusal surface often with more secondary wrinkling than in *Proconsul* s. str. Upper molars increase in size from M^1 to M^3 and premolars from P^3 to P^4, unlike *Proconsul*. No reduction of M^3. Lower molars and premolars also elongated. The molars have a marked wear gradient, such that M1 may have dentine exposed on the occlusal surface when M3 is only just coming into wear, unlike the condition in *Proconsul*. Strong lingual cingula are developed on all the upper molars and premolars, and the premolars also have a prominent distal cingulum. Zygomatic process is set very low over M1/2. The floor of the maxillary sinus is greatly extended. Mandibular body and symphysis relatively deep and robust.

Type species. *Proconsul* (*Rangwapithecus*) *gordoni* (Andrews), 1974 : 189 & 680.

Proconsul (*Rangwapithecus*) *gordoni* (Andrews 1974)

Diagnosis. A species of *Proconsul* intermediate in dental size between the siamang and pygmy chimpanzee; similar in size to *P. africanus*. Upper teeth similar to those of *P.* (*R.*) *vancouveringi* as described in the subgeneric diagnosis, differing only in their larger size. In the lower dentition the incisors are very high-crowned and narrow; the canine is high-crowned and bilaterally compressed; the P_3 is very bilaterally compressed with nearly parallel buccal and lingual sides; the P_4 is elongated; the M_1–M_3 are also elongated, the cusps are low, the buccal cusps are divided by deep buccal sulci like the condition in the gorilla, the occlusal ridges and buccal cingulum are

poorly defined, and secondary wrinkling is often present. P3–M3 lengths are: upper 40 mm, lower 44 mm for single specimens. M^1–M^3 length is 29 mm.

HOLOTYPE. Palate with complete left and right maxillary bodies and C–M^3. KNM-SO 700. (Pl. 3, fig. 1, p. 101.)

LOCALITY AND HORIZON. The Lower Miocene of Songhor with a few specimens from Rusinga and Mfwangano Islands, Kenya.

MATERIAL. 79 specimens which cover the complete mandible and maxilla except for the ascending ramus of the former and the nasal and zygomatic process of the latter.

Maxillary material. KNM-SO 401 with left P^4–M^1; MW 52 with left M^1–M^2 (this specimen is lost, but a cast is preserved in Nairobi).

Mandibular material. KNM-SO 374 with left P_4–M_2; SO 377 with left P_3–P_4; SO 463 with right M_1–M_3 (may be same individual as SO 700); SO 464 with right M_3; SO 486 with left M_2; SO 540 with left dp_4 and roots of M_1; SO 908 with right M_2; SO 1112 with left P_3–P_4, M_2, and roots of I_2–C, M_1, M_3.

Isolated teeth. M 16337, left M_3; the remaining specimens are listed in Tables 1–22.

DESCRIPTION. This species will be described together with the next, *P.* (*R.*) *vancouveringi.*

Proconsul (*Rangwapithecus*) *vancouveringi* (Andrews 1974)

DIAGNOSIS. A small species of *Proconsul* approximately the dental size of the siamang. It is like *P.* (*R.*) *gordoni* in morphology, as defined in the subgeneric diagnosis, but differs from it in size. The M^1 is significantly different from the M^1 of *P.* (*R.*) *gordoni* at greater than the 0·001 level of probability. The tooth row lengths are M^1–M^3, 22 mm, and P^3–M^3, estimated at 31 mm for a single specimen.

HOLOTYPE. Fragment of maxilla with left P^4–M^3. KNM-RU 2058.

LOCALITY AND HORIZON. The Lower Miocene of Rusinga and Mfwangano Islands and Songhor. It is also provisionally identified from the Middle Miocene deposits at Maboko Island. All the localities are in Kenya.

MATERIAL. Seven specimens as follows: KNM-RU 1778, maxillary fragment with left dp^4–M^1 and P^3–P^4 exposed in crypts; KNM-RU 1801, left M^1; KNM-RU 2058, maxilla with left P^4–M^3; KNM-MW 48, left M^3; KNM-SO 942, right M^3; KNM-SO 944, right M^1; KNM-SO 1134, right M^1. (Pl. 4, figs 1–2, 8, p. 103.)

Referred material. Three specimens from Maboko Island. KNM-MB 53 left P^3; KNM-MB 125 left M^1; KNM-MB 148 left dp^4.

DESCRIPTION. This species and *P.* (*R.*) *gordoni* are so similar in morphology that they can be described together. Their only major difference is one of size, but this difference is great enough for there to be little doubt that the species are distinct.

Maxilla and premaxilla (Table 1, p. 134–5). The premaxilla is restricted in extent in *P.* (*R.*) *gordoni* compared with modern apes, and is slightly less extensive than comparable-sized *P. africanus.* The nasal processes of the premaxilla are not complete on any specimen, but they appear to make up most of the wall of the nasal aperture. The body of the premaxilla is short, and the index (naso-alv. ht/M^1–M^3) $\times$ 100 is 35·0 %. The incisor roots are moderately procumbent, and the functional diastema would appear to be small, an anomalous situation in view of the large canines.

The alveolar process of the maxilla is shallow in both species. The maxillary sinus is greatly expanded posteriorly, although its forward limit is rather far back, above M^1. It is relatively wide, although the full width is not apparent in specimen SO 700 or RU 2058 because the zygomatic processes are broken off. The floor of the sinus is deeply excavated between the roots of the molars in a manner more nearly approaching modern pongids than any other Kenya Miocene species. This may be evidence of progressive sinus expansion in these species such as has occurred in living apes, particularly the orang-utan (Cave & Haines 1940). The tuberosities of the alveolar process are extremely short in both species, projecting 4 mm beyond the distal border of M^3 in SO 700. The greater palatine foramen is anterior in position, being opposite the mesial border of M^3.

Both these features are quite variable in modern pongids. The zygomatic process of the maxilla is set both relatively far anteriorly and inferiorly. Two specimens of *P.* (*R.*) *gordoni* and one of *P.* (*R.*) *vancouveringi* have the root of the zygomatic process above $M^{1/2}$. A double log regression of the height of the zygomatic process on the upper tooth row length distinguishes these two species from the regression for the three species of *P.* (*Proconsul*).

The overall size of the nasal aperture corresponds with that of *P. africanus*, but it appears relatively broader in relation to height. The palate is relatively long and narrow in *P.* (*R.*) *gordoni*. It widens posteriorly, and the width at M^3 is 114% of the width at M^1.

Mandible (Table 2, p. 136–7). The symphysis is preserved on one specimen of *P.* (*R.*) *gordoni* (KNM-SO 1112). It is extremely deep, and although gracile in its general construction has a massive superior transverse torus which gives a high value for the robusticity index [$(t/d) \times 100 =$ 56%]. The medial surface both above and below the torus is concave (Fig. 5) so that the superior torus is a shelf-like structure analogous to the inferior simian shelf of modern pongids. The mandibular body is deep and gracile. The buccal surface below M_1 runs slightly laterally for about 14 mm from the alveolar margin and then slopes vertically down to the inferior margin 12 mm beyond. The inferior border of the body is relatively sharply angulated in contrast to the bluntly rounded border of most pongids, in keeping with the greater body depth. The root of the mandibular ramus overlaps most of M_3.

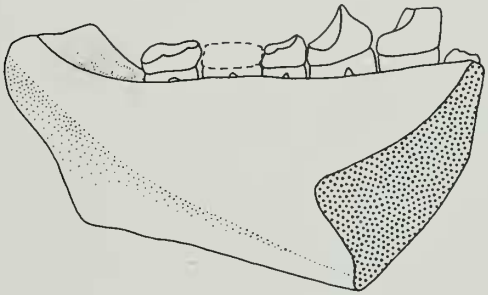


Fig. 5 The mandible of *Proconsul* (*Rangwapithecus*) *gordoni*, KNM-SO 1112, showing the almost shelf-like superior transverse torus. × 1.

Upper incisors (Tables 3–4, p. 138–140). The incisors are relatively high-crowned. The I^1 appears narrow as a result of buccolingual compression. The crown is strongly mesially skewed, and the incisive edge is relatively short, occupying the mesial $\frac{3}{4}$ of the crown. The lingual surface of the crown is prominently striated, particularly in the middle portion of the crown, and there is a well-developed lingual cingulum at the base. Wear is concentrated at or near the incisive edge; the top of the lingual surface is worn a little but on the available specimens the wear does not extend down onto the striated and swollen base of the crown.

The I^2 is a robust tooth, extremely mesially skewed so that the incisive edge has a slope of nearly 45°. The one specimen available is very worn, but the striations of the crown and development of the cingulum appear similar to the condition in I^1. The skewing of this tooth and the strong distal slope of the incisive edge both have the effect of increasing the available space for the top of the lower canine in occlusion. This could mean that the functional diastema between the upper canine and I^2, which is usually enlarged by the procumbancy of the incisors, may here be enlarged because the incisor crowns are skewed mesially.

Upper canine (Table 5, p. 141–3). The upper C is bilaterally compressed but rather low-crowned in comparison with length of crown. The long axis is only slightly oblique. There are no mesial ridges, but the distal ridge is very prominent, and is prolonged distally into a blade-like flange. This separates the broadly convex buccal surface from the slightly concave lingual surface. The mesial groove is very deep and is a striking feature of these teeth. There is only a slight distolingual cingulum present. Wear is both mesial and distal, the former producing a flat wear facet across

the mesial groove, and the latter a deep concave facet lingually across the distal flange, quickly obliterating it. So heavy is the distal wear that a distinct notch may be cut.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is bicuspid, as usual in pongids, but it shows signs of molarization. The buccal cusp is only a little higher than the lingual one and the crown outline is nearly rectangular, mainly the result of massive distal cingular development. The buccal half of the crown is only slightly larger mesiodistally than the lingual half. The mesial cingulum is strongly developed, and runs in parallel with the buccal ridge, so that the mesial fovea is well developed, nearly horizontal, but narrow. The ridges on *P.* (*R.*) *vancouveringi* are slightly better developed than on *P.* (*R.*) *gordoni*, and the cusps themselves are relatively cristodont, consisting of sharply-edged inverted triangles separated from each other by a deep V notch. There is a moderate lingual cingulum, starting at the midpoint of the lingual surface of the lingual cusp, and increasing distally until it runs into the large distal cingulum. The distal fovea enclosed by the cingulum is deep and well defined. There is also a slight buccal cingulum continuous with both mesial and distal ones, so that the tooth is almost completely encircled by cingulum.

The P^4 is even more molarized than the P^3 and is unusual in being larger than P^3. The increase is brought about by massive cingulum development. The cusps are nearly equal in size. The lingual cusp has two distinct ridges, one running mesially to the mesial cingulum and the other running without a break to the mesial side of the tip of the buccal cusp. Enclosed between the ridges is a narrow mesial fovea. Distally there are no ridges but there is considerable occlusal wrinkling, nearly as much as in M^3. The cingulum is very strongly developed. The mesial cingulum forms the margin of the mesial fovea, but continues past the mesial ridge of the buccal cusp to form a slight and discontinuous buccal cingulum. There is a large lingual cingulum, continuing from the lingual end of the mesial ridge of the lingual cusp and running into the large distal cingulum.

Upper molars (Tables 8–10, p. 147–153). The upper molars are four-cusped. The hypocone is large, and is often larger than some of the trigon cusps. The order in size is usually protocone–hypocone–paracone–metacone. The teeth are usually longer than broad. The relatively greater length is due partly to the expansion of the trigon, the paracone and metacone being widely separated, and partly to the large size of the hypocone. In *P.* (*R.*) *gordoni* the paracone is some way mesial to the protocone and the hypocone some way distal to the metacone, and this gives the teeth a diamond-shaped outline. The cusps have a sharp-edged 'crystalline' appearance and the ridges are well developed. Neither of the conules appears to be present. In *P.* (*R.*) *vancouveringi* the crown is more circular in outline and the protocone relatively much bigger. The hypocone is still large but it is smaller than the protocone.

The wear on the molars is a conspicuous feature of these two species, the wear gradient being very high. In *P.* (*R.*) *gordoni* SO 700 has the M^1 with moderate areas of dentine exposed on the lingual cusps, M^2 with evident signs of wear but no dentine exposed, and M^3 newly erupted with only slight traces of wear mesially. In *P.* (*R.*) *vancouveringi* RU 2058 is more heavily worn and has dentine exposed continuously along the lingual half of the crown of M^1; M^2 has dentine exposed on the protocone, and M^3 appears only slightly worn with no dentine exposed at all.

On M^1 the trigon is greatly expanded mesiodistally. The mesiobuccal ridge of the protocone divides into the mesiobuccal and distobuccal ridges of the protoconule and these both run slightly mesially to the bottom of the mesial border and half way up the border of the paracone respectively. Neither of them makes contact with the tip of the paracone. Between the two ridges is a narrow and inconspicuous mesial fovea. The distobuccal ridge of the protocone joins the lingual ridge of the metacone without a break to make the crista obliqua. The mesial and distal ridges of the paracone, and the mesial ridge of the metacone, are distinct but low and are deeply depressed, but not cut, by the buccal main groove.

The hypocone is very large and completely isolated. It stands on and is a part of the distal cingulum, which in *P.* (*R.*) *gordoni* appears to made up of two parts. The internal part stops short at the hypocone, but a thin external shelf of the distal cingulum does not stop at the distal margin of the hypocone, but continues around it and joins up with the lingual cingulum. Only the first of these is present in *P.* (*R.*) *vancouveringi*. The lingual cingulum is massive and is continuous all round the protocone. The main part of it merges into the hypocone but a small segment of it continues round the hypocone as already mentioned. The distal cingulum is similar to that of P^4

and ends buccally at a small angulation at the base of the cusp. A slight buccal cingulum is developed in the gap between the two buccal cusps. The cingulum is slightly beaded, and the occlusal surface of the whole tooth has fine wrinkles all over it. The wrinkling is quickly destroyed by wear and cannot have had much functional significance on this tooth.

The M^2 is a much larger tooth than M^1 and relatively broader, but is otherwise quite similar. The degree of wrinkling, which is much stronger, probably had more functional significance than that present in M^1. The lingual cingulum is not continuous around the hypocone, but breaks off as it reaches the distal border of the hypocone. The buccal cingulum is much more prominent and is continuous around the paracone.

The M^3 is a very large tooth, bigger than M^1 and M^2. It is also still relatively elongated although not as much as is M^1. There has been some morphological reduction, as the metacone and sometimes the hypocone are both reduced in size, but this is compensated for by great enlargement of the protocone. The trigon can hardly be distinguished except the mesiolingual portion of it between the protocone and protoconule which is sometimes developed. Apart from this the mesial and distal foveae appear continuous over the trigon. The cingulum is large, and the hypocone stands as an elevation on it, with no cingulum around its border. The buccal margin is conspicuous and shelf-like, and contacts the distal cingulum past the metacone. With the development of the protoconule, the elongation of the crown, and the moderate distal taper, the M^3 looks rather like a lower molar.

Lower incisors (Tables 11–12, p. 154–5). The lower incisors are very high-crowned and buccolingually compressed. They are quite exceptional for pongids in this respect and it is important to find incisors associated with posterior dentition in order to check the assignment to *P.* (*R.*) *gordoni* of the six isolated I_1 and seven I_2. The crowns are perfectly symmetrical and of simple construction with a narrow medial pillar on the lingual face but no striations. Wear is along the incisive edge only. There is no buccal wear such as would occur in overbite, and presumably the slight amount of wear lingually on the I^1 could be due to occlusion with the buccal edge of the incisive surface of the lower.

The I_2 is very like the I_1, and is more buccolingually compressed than is usual in pongid I_2s. The crown is only moderately mesially skewed and has a long incisive edge. A slight medial pillar is often developed. Wear is again confined to the incisive edge.

Lower canine (Table 13, p. 156–8). The lower canine is a very high-crowned, slender tooth. It has a moderate distobuccal curvature enhanced by the long mesial ridge. Only one specimen has the canine in place (SO 1112) and in this the crown is half broken away, but it does not appear that the crown is at all strongly laterally divergent. The root is very long and reaches nearly to the base of the mandible. The ends of the root sockets converge inferiorly and nearly meet below the incisor roots at the symphysis.

Lower premolars (Tables 14–15, p. 159–162). The P_3 is a very distinctive tooth. It has a sharply triangular crown, long and low-crowned. It is also strongly bilaterally compressed, so much so that the nearly straight buccal and lingual faces are parallel, joining front and back in bluntly rounded surfaces. The lingual face of the crown between the mesial and lingual ridges is flat, and as the distolingual ridge is nearly as far distal as the distal ridge, the lingual face is greatly expanded. The ridges are massive and rounded rather than sharp and distinct, and they enclose a small and shallow distal heel which also connects up with the slight lingual cingulum. There are too few specimens to be able to conclude much on the kind of wear on the P_3, but, from its morphology and that of the upper and lower C, it is likely that at least a moderate degree of sectoriality is present.

The P_4 is a bicuspid tooth that is longer than broad. Linked with this elongation the crown is less obliquely set in the tooth row. The buccal and lingual cusps are equal in height, the buccal one being slightly in advance of the other. They are not connected by any ridge, but as they are set so close together in the narrow crown a depression is isolated mesially. The crown is elongated distally with a prominent distal cingulum, and this region has much secondary wrinkling. The buccal cingulum is also prominent, although usually not continuous. It is largest on the mesiobuccal angle of the buccal cusp, may continue thinly around this cusp, and is large again distal to this, where it joins the distal cingulum.

Lower molars (Tables 16–18, p. 163–170). The M_1 is an elongated narrow tooth. It is set rather obliquely with the buccal cusps mesial to the corresponding lingual ones. The trigonid ridges are poorly developed so that the trigonid basin is not separated from the talonid basin. There is a very slight trace of the distal trigonid ridge but it appears no stronger than the secondary wrinkling which is a feature of the talonid surface. The buccal ridges are strongly indented into the talonid basin, so that the buccal cusps are isolated from each other. Large diamond-shaped foveae are produced buccally with the buccal margin of the crown being provided by the cingulum. The system of grooves follows the usual pattern, but the occlusal surface shows a tendency to be broken up into secondary wrinkles and folds. The cingulum is strongly developed, but is less shelf-like and fills the gap between the two buccal cusps. When it is completely unworn the cingulum may be beaded. The cusps do not project very high above the occlusal plane, so with wear they are quickly worn down to this level. Wear initially is at the tips of the cusps, but as it continues the elaboration of the crown comes into effect as the wear crosses the folds and wrinkles in the trigonid and talonid basins. The wear gradient is similar to that described for the upper molars.

The M_2 is similar to M_1 in general morphology and in the indented buccal margin. The trigonid basin is completely undifferentiated from the talonid. The only trigonid ridge is a slight mesial one. There is a moderate entoconid–hypoconulid ridge with a distal fovea beyond it. The wrinkling and folding are conspicuous, particularly in the region of the trigonid and mesial part of the talonid. The hypoconulid is more buccally placed, and is isolated similarly to the other buccal cusps with a large triangular infilling of cingulum between it and the hypoconid.

The M_3 is a very large tooth, much larger than M_1 or M_2. The M_3 has very strongly developed folding and wrinkling covering the whole occlusal surface. There is no division into separate compartments as the ridges are poorly developed and appear as part of the secondary folding. The hypoconulid is buccally placed exactly in line with the protoconid and hypoconid, and is isolated in the same way as they are. There is no reduction of the distal end of the tooth so the crown lacks the triangular shape characteristic of the M_3 in species of *Proconsul* s. str. The buccal cingulum is the most strongly developed of the lower molars and is nearly continuous along the buccal edge.

Deciduous dentition (Tables 19–21, p. 171–3). One isolated di^2 is referred to *P.* (*R.*) *gordoni* on the basis of size. It is high-crowned and mesiodistally compressed. The tip is pointed and there is only a very short incisive edge mesial to the tip. The lingual cingulum is relatively well developed.

Two isolated dc are referred to *P.* (*R.*) *gordoni* on the basis of size. They are low-crowned, featureless teeth. There is no ridge or groove formation. They have a massive lingual cingulum, shelf-like along most of its length and extremely swollen lingually. There is a slight elevation of the cingulum about one third of the way distally from the mesial origin of the cingulum.

The dp^3 is a bicuspid tooth. The specimen is not associated with any permanent teeth and its allocation to *P.* (*R.*) *gordoni* is based on size. The buccal cusp is much larger than the lingual one, but is so heavily worn it is difficult to say how much taller it was. There is a faint ridge connecting the cusps. Mesial to it the mesial cingulum is fairly strongly developed and distally the distal cingulum is more strongly developed, although not to the extent that might have been expected for a milk tooth of this species.

The dp^4 of *P.* (*R.*) *vancouveringi* is a most unusual tooth. It is extremely elongated; the breadth/length index is 85·7%, much lower than for M^1. Apart from that, the crown is similar to the associated M^1 except that it is lower-crowned, the cusps are lower, and the lingual cingulum is poorly developed. The measurements for this specimen (KNM-RU 1778) are mesiodistal length 6·3 mm and buccolingual breadth 5·4 mm. A second specimen of this tooth was recovered from the later depqsits of Maboko Island (KNM-MB 148). It is almost identical in size and morphology to the Rusinga specimen despite the probable age difference of several million years between the two sites. A single tooth, SO 945, might be a dp^4 of *P.* (*R.*) *gordoni*, but it is very uncertain and no account can be given until better material is available.

The dp_4 is a molariform tooth with very distinctive morphology. It is elongated and narrow. The protoconid is far mesial to the metaconid and has a mesial trigonid ridge running mesiolingually to a very slight elevation that probably represents the paraconid. The trigonid basin is well developed and triangular in shape, and mesial to it is a small mesial fovea. The mesial end

of the tooth is therefore very long and constitutes part of the elongation of the crown. The rest is made up by the lengthened talonid, a relatively large space separating the protoconid–metaconid from the hypoconid–entoconid. The hypoconulid is small and does not much affect the length of the crown. The effect of narrowness of the crown is enhanced by the way the cusps are set in from the lingual and buccal edges, particularly the latter. In addition, the buccal cingulum is only slightly developed.

Remarks. *Proconsul* (*Rangwapithecus*) *gordoni* and *P.* (*R.*) *vancouveringi* are so similar that there is little doubt that they are closely related. The question that remains to be answered, however, is whether they are specifically distinct. Such a distinction must be based almost entirely on the size difference between them, but there is an additional difference in their geographical ranges. The size differences are indicated in Tables 6–10 (p. 144–153) and in Figs 12–16, and these give an indication of the degree of difference between them, but the only sample large enough to enable a statistical test to be made is that for M^1. A sample of 13 is available for this tooth, and these divided clearly into two groups on the bivariate (breadth/length) plot in Fig. 14 (p. 182). Significance tests on the two samples gave values of *t* of 9·9 for mesiodistal length and 13·8 for buccolingual breadth, and, therefore, probabilities of very much less than 0·001 that the two samples represented one statistical population (Andrews 1974 : 188). Furthermore, the two samples differ in their distributions. That referred to *P.* (*R.*) *gordoni* is known almost exclusively from Songhor (72 specimens) with only one good specimen known from Mfwangano and a few isolated teeth from Rusinga. The much smaller sample of *P.* (*R.*) *vancouveringi* is known by isolated teeth from Rusinga, Mfwangano, and Songhor, but the two more complete specimens are both from Rusinga. This largely allopatric distribution, coupled with the big size difference, is felt sufficient to justify the distinction at the species level.

Genus *LIMNOPITHECUS* Hopwood 1933

Diagnosis. Primitive apes of Miocene age from Africa. Dental size slightly smaller than *Hylobates*. Central incisors relatively large and broad. Canines well developed, the lower with short mesial ridge and very asymmetrical. P^3–P^4 low-crowned, cusps of approximately equal size. P_3 single-cusped but low-crowned, P_4 elongated. Molar cusps low and rounded. Distinct buccal cingulum on the lower molars, occlusal ridges poorly developed, and distinct size increase from M_1 to M_3. Distinct lingual cingulum on the upper molars, cingulum not crenulated, slight protoconule developed, occlusal ridges moderately well defined, and increase of molar size in sequence M^1–M^3–M^2. The M^3 is slightly reduced in size. P_3–M_3 length averages 26–27 mm. The mandible is relatively short.

Type species. *Limnopithecus legetet* Hopwood 1933 : 97.

Limnopithecus legetet Hopwood 1933

1933 *Limnopithecus legetet* Hopwood : 97.
1943 *Limnopithecus evansi* MacInnes : 153.
1963 *Pliopithecus* (*Limnopithecus*) *legetet* (Hopwood) Simons : 881.

Diagnosis. As for genus.

Holotype. Distorted mandible with M_1–M_2. BM(NH) M 14079.

Locality and Horizon. The Lower Miocene of Songhor, Koru, Ombo, and Rusinga Island; and the Middle Miocene of Fort Ternan and Maboko, Kenya. The Oligo-Miocene of Bukwa, and the Lower Miocene of Napak, Uganda.

Material. 116 specimens which cover the complete dentition, the premaxilla, the portion of the maxillary body between C and M^1, and the mandible except for the ascending ramus.

Maxillary material. KNM-SO 421 with left P^3; SO 443 with right C–M^1; SO 535 with right M^2–M^3; SO 536 with right dp^3–dp^4 and M^1; SO 537 with left M^1–M^2; SO 538 with left C–P^3. (Pl. 4, fig. 7, p. 103.)

Mandibular material. M 14079 with right M_1–M_2; M 14080 with left dp_3–dp_4; M 14284 with right P_3–P_4; M 32227 with left P_3; KNM-SO 376 with right M_1; SO 385 with right P_4–M_2; SO 386 with left P_3 and right M_1–M_3; SO 387 with left M_1–M_2; SO 388 with right M_2; SO 444 with right M_2–M_3; SO 455 with right M_3; SO 482 with right M_1–M_2; SO 532 with right M_2–M_3; SO 533 with right P_3; SO 534 with right M_1–M_2; SO 1073 with left dp_3–dp_4; SO 1075 with right C–P_3; KNM-KO 6 with right M_3; KO 7 with left M_2; KO 8 with I_1–M_2; KO 11 with dp_3; KNM-RU 1708 with right M_2–M_3; RU 1916 with right P_3–P_4; RU 2078 with right M_1; KNM-OM 35 mandibular symphysis. (Pl. 4, figs 5–6, p. 103; Pl. 6, p. 119.)

Isolated teeth. M 14332, right I^1; the remaining specimens are listed in Tables 1–22.

Referred material. 37 specimens attributable to *L. legetet* are known from Napak, Uganda. Some of these are mentioned by Bishop (1964 : 1329–1330), and one, UM-P 64-02, has been recently described by Fleagle (1975). Thirteen specimens from Fort Ternan are provisionally referred to *L. legetet*. There are KNM-FT 19–24, left mandible with C–M_3 and associated right P_4–M_2 and M^3 (Pl. 6); FT 11 left I^1; FT 12 edentulous mandible; FT 14 immature mandible with M_1; FT 15 left C; FT 17 left M_1; FT 18 right P_4; FT 25 right I_2. Seven specimens from Maboko Island are provisionally referred to *L. legetet*, KNM-MB 109 M^2, 147 M^1, 149 M_2, 151 I^2, 152 M^3, 153 I_2 and 156 C^1.

Description. This description is based entirely on the Kenya specimens. There are a number of specimens probably belonging to this species from Napak, Uganda, but I have not been able to include these here.

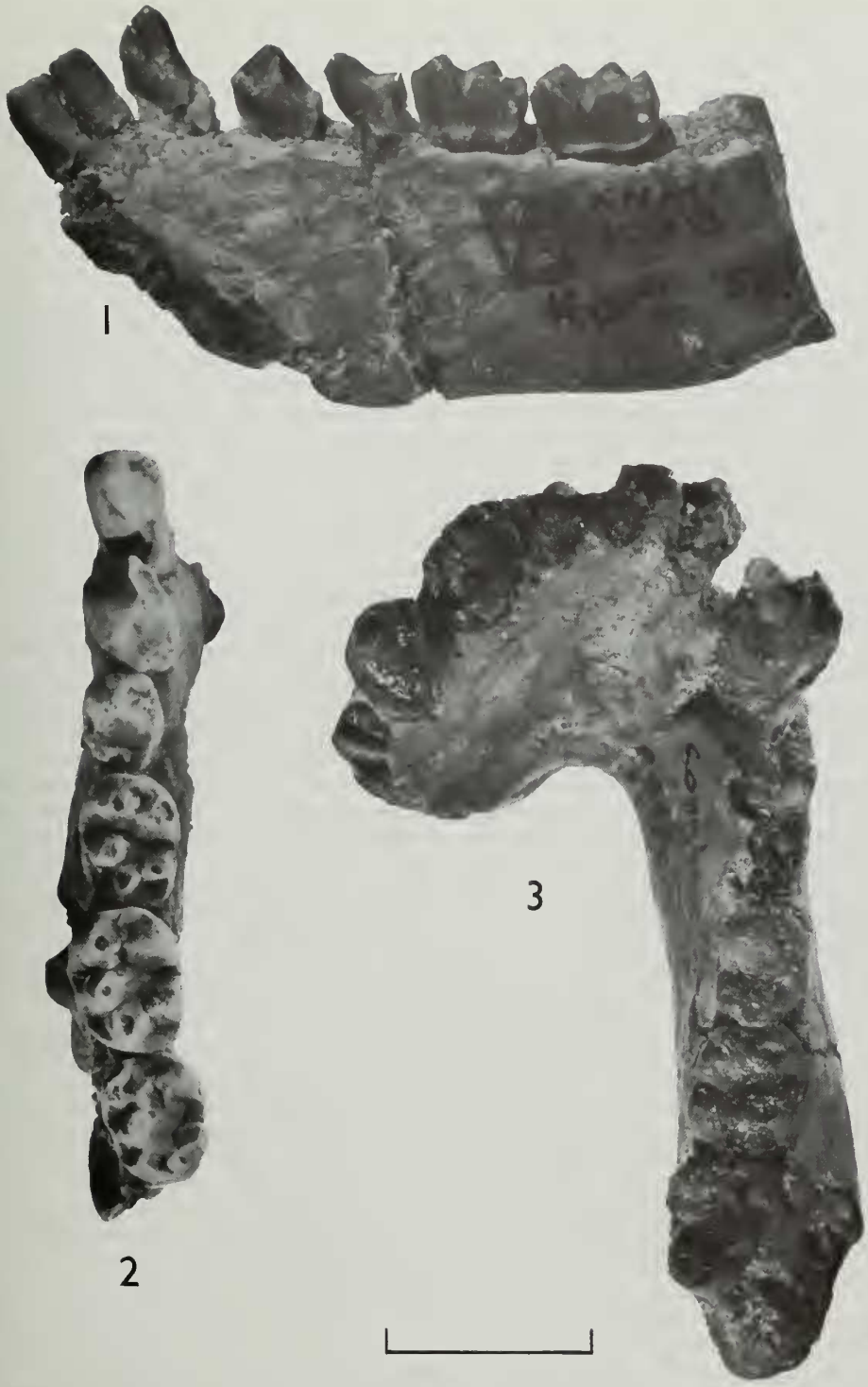
Maxilla and premaxilla (Table 1, p. 134–5). Maxillary specimens are fewer and more fragmented than the mandibular ones. Only one specimen has the molars associated with any of the anterior teeth. The premaxilla is preserved on a number of specimens, but is never complete. The nasal process ascends the side of the nasal aperture, and it looks as though it may connect up with the nasal bones, i.e. complete the side of the aperture, but all the specimens are broken before this point is reached so it is impossible to establish this. It appears that the aperture was probably high and narrow.

The alveolar process of the maxilla is low and gracile. On the large specimens there are relatively prominent canine juga associated with the canine root and distinct concavities posterior to them (canine fossae). The maxillary sinus is long and narrow. Its anterior end is above P^4 and it extends beyond M^3. It is excavated between the roots of M^2 and M^3, but there is no division into loculi. It does not seem to extend laterally into the zygomatic process, and medially it is limited by the nasal cavity which may be relatively broad. In this it is like the condition in dryopithecines and differs from that of *Dendropithecus macinnesi*, in which the sinus floor is wide and the nasal cavity narrow. The root of the zygomatic process is above M^2 and does not appear to be close to the alveolar border. On two specimens the zygomatic process still curves laterally at 4 mm above the alveolar border, so the actual height must be greater than this. On the one specimen measurable it is 5·6 mm.

Mandible (Table 2, p. 136–7). Despite the large sample the mandibular symphysis is preserved entire on only a few specimens. Its morphology is similar to that of the other Kenya dryopithecines. The internal surface slopes evenly down from the incisor alveolus and reaches its most posterior extent slightly below the midline at the superior transverse torus; from there it slopes very slightly anteriorly with a broad shallow genial concavity. The development of genial pits varies but usually consists of two pairs, the pairs being divided by the symphysis. The most posterior extent of the symphysis reaches the level of mid-P_3. The anterior surface of the mandible on either side of the symphysis is gently convex, but on the specimens with large canines the canine juga are prominent so that the anterior face is flattened and sharply divided from the posterior body of the mandible.

Plate 6

Fig. 1 *Limnopithecus legetet*. Right mandible with I_1–M_2, lingual view (KNM-KO 8).
Fig. 2 cf. *Limnopithecus legetet*. Left mandible with C–M_3, occlusal view (KNM-FT 20).
Fig. 3 *Limnopithecus legetet*. Mandible with left P_3, right C and M_1–M_3, occlusal view (KNM-SO 386).


1
2
3

The mandibular body is fairly robustly built. It becomes slightly shallower posteriorly. Laterally the mental foramen is set below P_3/P_4 about $\frac{3}{8}$ of the way up from the inferior border. The lateral surface of the body is slightly concave between the canine juga and the root of the ramus. The latter rises steeply and overlaps most of the last molar. The lingual surface of the body is marked by the mylo-hyoid line which is often extremely prominent; it passes down to the inferior border of the body and crosses the symphysis along the inferior edge. The mandibular ramus is not preserved on any specimen. The root of it overlaps M_3 and at this point is rising nearly vertically, so it is likely that the whole ramus was nearly vertical and lacked any great posterior slope.

Upper incisors (Tables 3–4, p. 138–140). The I^1 is a broad spatulate tooth. The crown is mesiodistally appreciably broader than thick. It is also higher than broad but not by much and the effect is of a low-crowned tooth. The lingual surface is flat to slightly concave, with a rounded swelling arising from a prominent basal cingulum. The large cingulum, which leads into mesial and distal marginal ridges, makes the lingual surface appear hollowed out. The height of the lingual cingulum varies but it is usually quite high so that it limits the lingual face. Wear begins along the incisive edge and on the lingual surface of the crown immediately above it. In its early stages it hits up against the lingual swelling and slowly cuts into it. Eventually wear obliterates all trace of the swelling and cuts a broad channel through the lingual cingulum.

By contrast with the I^1 only one specimen of the I^2 is known. It is assigned to this species because it is small, relatively broad, and low-crowned. The mesiodistal dimension is actually larger than the buccolingual one. The lingual face is nearly flat, and is bordered by the same combination of basal cingulum and mesiodistal marginal ridges seen in I^1. The crown is strongly mesially angulated, but even though this specimen is unworn there is a considerable incisive edge.

Upper canine (Table 5, p. 141–3). The crowns are bilaterally flattened and blade-like in appearance. The roots are long and often have a pronounced buccal curve. The crown has a rounded and indistinct mesial ridge, which forms the buccal margin of a shallow mesial groove. There is a very broad and rounded lingual pillar (rather than a ridge) immediately distal to the mesial groove, and distal to this the crown is flat to slightly concave. The distal ridge is more strongly developed and is incipiently blade-like. The buccal surface of the crown is evenly convex. The crown appears symmetrical when viewed buccally, but there is a slight distal curve to the tip of the crown. The lingual cingulum is well developed. It is largest mesially and where it contacts the mesial ridge a tiny tubercle is sometimes present. Distal to this it forms the end of the mesial groove, and there is a distinct elevation of the cingulum at the top of the lingual pillar. Distally the cingulum is low and narrow.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is a bicuspid tooth. The buccal cusp is bigger and more conical than the lingual one but the difference in height is not marked. The crown outline is nearly rectangular, and the crown is only slightly longer buccally than lingually because there is a small lingual and bigger distolingual cingulum developed that fills out the lingual side of the crown. There is a shelf-like distal cingulum ending buccally in a small tubercle on the distal ridge of the buccal cusp. There is no ridge developed on the occlusal surface.

The P^4 is very similar to the P^3 and is slightly the larger in the one specimen on which both teeth are present. The two cusps are nearly equal in height, and are connected by a low transverse ridge running between the tips of the cusps. There is a slight lingual cingulum running from the mesial edge of the lingual cusp, becoming wider distally, and the distal cingulum is shelf-like.

Upper molars (Tables 8–10, p. 147–153). In M^1 the paracone and metacone are equal in size. The protocone is larger in basal outline but even before wear it is a little lower than the paracone and the metacone; it is situated just distal to the line of the paracone. The development of the hypocone is variable: in some it appears as part of the cingulum and is continuous with it, although it has a conical outline like the other cusps, and it is nearly as big as the paracone. In others, however, the hypocone is more independent of the cingulum and even has a slight cingulum developed on its lingual border. In all cases the hypocone lies slightly distal to the metacone and slightly lingual to the protocone.

The trigon is well defined although the trigon ridges are low and rounded. The mesiobuccal ridge of the protocone is a massive ridge running obliquely forwards towards the protoconule. This is sometimes absent but usually it can just be seen. The mesiobuccal ridge of the proto-

conule is short so that the mesial fovea is extremely restricted and could have had little functional purpose in occlusion. The distobuccal ridge of the protocone branches almost immediately into a buccal branch to the metacone (crista obliqua) and smaller distal branch to the hypocone. The distal fovea is well developed and is divided from the distal cingulum by a well-marked transverse ridge running from the distal edge of the tip of the metacone to the bottom of the mesial border of the hypocone. The lingual cingulum is well developed. It starts on the mesial border of the protocone, reaching its maximum thickness on the lingual border of this cusp. It is sometimes continuous around the hypocone, joining up with the well-developed distal cingulum just described. There is also a slight buccal cingulum, most strongly developed in the interval between the paracone and the metacone.

There is no complete upper tooth row preserved, but on the basis of comparison of single teeth it appears that M^2 is the largest molar. The metacone on M^2 is slightly reduced in size and is lingually displaced relative to the paracone so that the distobuccal corner of the tooth is slightly cut away. The hypocone is also reduced relative to the protocone and may also be *lingually* displaced so that the distolingual corner is extended. The occlusal ridges are more distinct than on M^1, and in particular the mesial branch of the mesiobuccal ridge of the protocone is often better developed. The cingulum is more strongly developed than in M^1, but is similar in morphology and is always most strongly developed lingually.

Most of the differences seen between M^2 and M^1 are even more exaggerated in M^3. The protocone is very large and the hypocone small and sometimes vestigial. The metacone is usually present, but very reduced. The cingulum forms a complete ring around the tooth, and it is largest distolingually.

Lower incisors (Tables 11–12, p. 154–5). The I_1 crown is well preserved in the half mandible KO 8. It has a symmetrical, relatively broad mesiodistal crown. It is also relatively low-crowned although still higher than broad. The crown morphology is simple. The lingual face is slightly concave and lacks any cingulum or lingual swelling. The buccal face is gently convex. Wear is concentrated along the incisive edge, and in one specimen passes down on to the lingual face.

The I_2 is also relatively broad mesiodistally, having a similar breadth/length index as in I_1, but in this case it is even more remarkable a feature, for usually in pongids the I_2 is relatively much narrower than the I_1. The morphology is also very close to that of I_1, except for the asymmetry resulting from the bulging of the distal edge of the crown.

Lower canine (Table 13, p. 156–8). The canine is variable in size. In some cases where a small canine is associated with small posterior teeth and a gracile mandible, and a large canine with large posterior teeth and robust mandible, it is possible to attribute the variability to sexual differences, but there are many cases where the sex is uncertain. It is bilaterally compressed and the long axis is set obliquely to the line of the molar–premolar tooth row. The mesial ridge is extremely short and gives the crown a skewed and incisiform look. Lingual and distal ridges are faintly outlined, and the former also meets the cingulum at a distinct elevation. The lingual cingulum is narrow but quite distinct. It is most strongly developed at its mesial end, and it diminishes rapidly beyond its contact point with the lingual ridge so that the distal end of the crown, which is slightly prolonged into a heel-like process, apparently has no cingulum.

Lower premolars (Tables 14–15, p. 159–162). The P_3 has one principal cusp. It is only moderately bilaterally compressed, unlike the C, and the long axis is only slightly obliquely placed relative to the molar–premolar tooth row. It is set close to the canine, and on some specimens the mesial end of P_3 overlaps the distal end of the C. The pattern of three distinct ridges on the occlusal surface is very characteristic of this species. The mesial and distal ridges arise from the tip of the cusp and follow the line of the main axis of the molar–premolar series to the mesial and distal borders of the tooth. There they link up with a narrow lingual cingulum which completes a semicircle around the lingual border. More or less perpendicular to these two ridges is a lingual ridge, homologous probably with the distal ridge of the primitive trigonid of the molar. Where it meets the lingual cingulum the latter is raised up in a distinct tubercle.

On all available specimens the crown of P_4 is longer than broad. There is some indication that on the larger specimens the crown is relatively broader but more material is needed to be certain. Related to this, the long axis of the tooth is slightly oblique on the large specimens but is in line

with the molar tooth row in the small gracile specimens. The two cusps are approximately equal in size and height. The buccal cusp is set in front of the lingual cusp, and they are connected by a moderately distinct transverse ridge. There is a small fovea mesial to this ridge. Distally there is an elongated fovea bounded on each side by distal ridges from the two main cusps, and at the distal angle of the fovea these ridges are raised into low inconspicuous tubercles. There are slight traces of buccal cingulum on the mesiobuccal face of the buccal cusp, and along the buccal edge of the distal basin. The cingulum becomes higher distally until it contacts the distobuccal tubercle which is probably then a cingular structure.

Lower molars (Tables 16–18, p. 163–170). The M_1 is five-cusped and always longer than broad. It is the smallest molar, and differs morphologically from the others by having the hypoconulid centrally placed and the talonid usually broader than the trigonid. The protoconid is often slightly in advance of the metaconid. It is set relatively far in from the buccal border and this distance is increased by the development of the buccal cingulum, which is thickest at the buccal border of the protoconid. The metaconid, the other trigonid cusp, rises steeply up from the lingual border of the tooth. The mesial and distal trigonid ridges enclose a small trigonid basin which is often referred to as the anterior fovea. That it is actually the trigonid basin, however, is established by the ridge homologies. In some specimens the basin is poorly developed or even absent altogether.

The talonid cusps of M_1 all appear isolated. On some specimens two longitudinal ridges are faintly apparent between the protoconid and the hypoconid and between the metaconid and the entoconid, but both are deeply cut by sulci. The hypoconulid is completely isolated. There is no sign of any ridge connecting hypoconulid and entoconid, and as a result of this there is no distal fovea differentiated. The development of the cingulum varies but is usually well developed on the buccal side of the lower molars. It is most strongly developed on the buccal border of the protoconid and in the interval between the protoconid and hypoconid.

The M_2 is the broadest of the molars. It is bigger than M_1 but smaller than M_3. It is similar in morphology to M_1 but the trigonid and talonid ridges are slightly better defined. The trigonid basin is nearly always apparent. The cingulum is more strongly developed, again on the protoconid and in the interval between it and the hypoconid. On one specimen there is a small cuspule on the cingulum between the protoconid and hypoconid, and in this specimen the cingulum is continuous around the buccal border of the hypoconid. The hypoconulid varies in position, but is more buccally placed than in M_1.

The M_3, the biggest of the molars, is elongated and relatively narrow. The trigonid ridges are no better developed than in M_2, but the talonid ridges are absent altogether and the enlarged hypoconulid occupies the whole of the distal end of the tooth. The cingulum is continuous buccally past the protoconid and hypoconid, but always remains narrow.

Deciduous dentition (Tables 19–21, p. 171–3). The di^1 is a low-crowned spatulate tooth. The lingual surface has a massive lingual cingulum merging into a short pointed lingual pillar that stops before it reaches the incisive edge. The buccal surface is smooth and rounded. In both specimens available the mesiodistal length exceeds the buccal height.

The upper dc is a low-crowned tooth. The lingual cingulum is massive and more shelf-like than in the di^1. One of the specimens has a slight lingual elevation of the cingulum connecting up with a lingual ridge to the tip of the crown but the other has no trace of either of these features. There is no mesial groove. The mesiodistal length is approximately equal to the buccal height.

The dp^3 has a marked buccal elongation, and the buccal cusp is considerably higher than the lingual one. There is an indistinct ridge connecting the two cusps. The distal cingulum is slightly developed. There are two buccal roots and a single lingual one.

The dp^4 is almost identical to M^1 except that it is smaller, lower crowned, and has thinner enamel. Ridge development is similar but the protoconule cannot be seen. The lingual cingulum is less shelf-like but relatively larger than on M^1. The crown is less rectangular than M^1 as the mesial and distal surfaces converge towards the lingual border.

The crown of dp_3 is almost bicuspid, although the buccal cusp is much larger than the lingual one. The cusps are joined by a sharp ridge running distolingually from the main cusp to the lingual one. There is a ridge running mesially from the buccal cusp to the mesial point of the crown, where there is a slight tubercle developed. The distal ridge of the buccal cusp is less

distinct, but it also has a tubercle at its distal end. The lingual cingulum is well developed. The crown is elongated and bilaterally compressed.

The dp_4 is similar to M_1 but more elongated. The talonid width is relatively greater than the trigonid width, and the protoconid is well in advance (mesially) of the metaconid. There is no sign of paraconid development. The buccal cingulum is only slightly developed.

REMARKS. The taxon *Limnopithecus legetet* was first described from very inadequate material from Koru (Hopwood 1933). It was said at that time that it was a gibbon-like primate, in contrast to the chimpanzee-like morphology of *Proconsul africanus*. Little evidence was put forward to substantiate this view, but the contrary evidence of the differences between the milk dentitions of *L. legetet* and *Hylobates* was pointed out (Hopwood 1933a : 440). It was not mentioned, however, that *L. legetet* resembled pongids rather than hylobatids in the milk dentition.

In 1943 a second species, *L. evansi*, was described (MacInnes 1943 : 152). That such a split could be made depended solely on the inadequacy of the material on which *L. legetet* had originally been based, and discovery of further material made it quite obvious that the specific distinction of *L. evansi* was invalid (Clark & Leakey 1951).

The description of a third species, *L. macinnesi* (Clark & Leakey 1951), which was also said to have many hylobatine characters, seemed to confirm the family classification of *Limnopithecus*. However, in their discussion on the origin of *Proconsul*, Clark & Leakey (1951) concluded that an ancestor of *Proconsul* might have looked something like *Limnopithecus* and that the two genera were really not greatly different. They considered that *L. macinnesi* was too specialized in its C–P_3 morphology, but that as these specializations were absent in *L. legetet*, the latter served as a good model of the ancestral condition for *Proconsul* (Clark & Leakey 1951 : 111). This is so true that it is surprising that they put the two species of *Limnopithecus* together at all, for while *L. legetet* is morphologically very like the much larger *Proconsul* species, *L. macinnesi* has many features that link it with the gibbons.

What has been so misleading in this whole question of the status of *Limnopithecus* is a largely unconscious bias towards linking species of similar size. Size is not a valid criterion for a generic diagnosis, and it was not used explicitly in the earlier diagnoses of *Limnopithecus*, but because the morphological variation between all hominoid species, both fossil and Recent, is so small, species of similar size tend to look very much alike and so are grouped together. This essentially was the basis for the original linking of *L. legetet* and '*L.*' *macinnesi*, both with each other and with the Recent gibbons. If size is ignored, however, and morphological similarities alone considered, it is at once evident that the greatest degree of similarity of *L. legetet* is with *Proconsul africanus*, not with '*L.*' *macinnesi*. This is shown by the following list of characters which are shared by *L. legetet* and *P. africanus*, but for which '*L.*' *macinnesi* has the contrary condition. Maxillary sinus long and narrow; nasal aperture broad; mandibular symphysis with a superior transverse torus; incisors broad and low-crowned; I^1 spatulate; C rounded, not bilaterally compressed, and lacking a double mesial groove on the uppers; P_3 triangular in shape, not bilaterally compressed, grinding function rather than sectorial, low-crowned; M^1 square, not very much broader than long; M^3 very reduced relative to M^2; M_1 with strong buccal cingulum; M_3 elongated, crown compressed distally, and with a large heel-like hypoconulid.

In contrast to this there are only a few characters in which *L. legetet* resembles '*L.*' *macinnesi* to the exclusion of *P. africanus*. These are: C with short mesial ridge; P_4 elongated, longer than broad; and molars with low bulbous cusp formation. None of these are absolute differences from other species of dryopithecine, and they are of relatively minor significance compared with the extreme sectorial development of the C–P_3 complex of '*L.*' *macinnesi*. The postcranial material also, although it is not being covered in this paper, and there are only two specimens available for *L. legetet*, indicates an affinity between the latter and *P. africanus*, very different from the elongated and gracile long bones of '*L.*' *macinnesi* (Clark & Thomas 1951). The latter, indeed, is the strongest evidence for linking '*L.*' *macinnesi* with the ancestry of the gibbons, and it is on this basis, together with the sectorial specializations just mentioned, that it is retained in the Hylobatidae (see next section) while *L. legetet* is removed to the Pongidae, Dryopithecinae.

Family **HYLOBATIDAE** Blyth 1875

Genus ***DENDROPITHECUS*** Andrews & Simons 1977

DIAGNOSIS. Small anthropoid apes approximating in dental size to the siamang. Incisors high-crowned and strongly mesiodistally compressed. Canines blade-like, in males with double mesial grooves, showing a striking degree of sexual dimorphism. P_3 sectorial *sensu stricto*, as in gibbons. P^3 has strongly projecting buccal cusp. Lower molars have the cusps arranged around the periphery of the crowns, connected by well-defined ridges and enclosing large trigonid and talonid basins. Buccal cingulum of lower molars slightly developed. Upper molars of simple construction, with well-defined trigon and relatively small hypocone. Prominent lingual cingulum. M_3 slightly larger than M_2. M^3 usually reduced. Palate long and narrow and maxillary sinus well developed. Body and symphysis of mandible robust, well-developed superior transverse torus and usually also an inferior torus projecting posteriorly at least to the extent of the superior torus and often further. Dentally very similar to *Pliopithecus*, but having higher-crowned incisors, more strongly bilaterally compressed canines, more sectorial P_3, more projecting buccal cusp on P^3, and lower molars with stronger ridge formation and delineation of the talonid basin. Differs from *Pliopithecus* postcranially, particularly in the length and slenderness of the long bones. All the postcranial bones lack conspicuous muscular markings.

TYPE SPECIES. *Dendropithecus macinnesi* (Clark & Leakey), 1950 : 262.

Dendropithecus macinnesi (Le Gros Clark & Leakey 1950)

1950 *Limnopithecus macinnesi* Clark & Leakey : 262.
1963 *Pliopithecus* (*Limnopithecus*) *macinnesi* (Clark & Leakey) Simons : 881.
1970 *Aegyptopithecus* sp. Simons; Andrews : 539.
1977 *Dendropithecus macinnesi* (Clark & Leakey) Andrews & Simons : 162.

DIAGNOSIS. As for genus.

HOLOTYPE. The greater part of both mandibular bodies, lacking the symphysis, and containing P_3–P_4 and M_2–M_3 on both sides. BM(NH) M 16650.

LOCALITY AND HORIZON. The Lower Miocene of Rusinga, Mfwangano, Karungu, Songhor and Koru, Kenya.

MATERIAL. 160 specimens which cover all of the maxilla and dentition and the mandible except for the ascending ramus. Postcranial material in direct association with cranial remains are known.

Maxillary material. KNM-RU 1774 with left and right C–M^3; RU 1799 with right M^1–M^3 and associated fragmentary skull fragments; RU 1806 ten associated teeth; RU 1849 associated upper and lower dentition with left I^1 and right I^1–M^3; RU 1850 associated upper and lower dentition, complete palate with C–M_3 both sides; RU 1915 with right M^2–M^3; RU 2086 with right P^4–M^2; KNM-SO 539 with left I^1–P^4. (Pl. 2, fig. 5, p. 97.)

Mandibular material. M 16650 with left and right P_3–P_4 and M_2–M_3; M 14083 symphysis with left P_3; KNM-RU 900 with right I_1–I_2 and left I_1–M_1; RU 1725 with right M_1–M_3; RU 1726 with right M_2–M_3; RU 1727 with left P_3–M_1; RU 1804 with right M_1–M_2; RU 1810 with roots C–C and right P_3; RU 1844 with left M_2; RU 1849 with right M_2–M_3 (see maxilla); RU 1850 with left M_2 and right M_1–M_3 (see maxilla); RU 1857 with right P_4–M_1 and M_3; RU 1893 with right P_3–P_4 and M_2; RU 1901 with right M_1–M_3 and nine associated teeth; RU 1925 with left M_1; RU 1935 with right P_3–P_4; RU 1962 with left C; RU 1972 with right C–P_3; RU 1978 with left M_3; RU 2001 symphysis; RU 2015 left and right bodies with right P_3–M_3 and left M_2–M_3; KNM-MW 51 symphysis with roots of right P_3–M_1; MW 53 with left P_3–M_2; KNM-SO 378 with right P_4–M_3; SO 405 symphysis with right C and two isolated teeth; SO 530 with right P_3 and M_1–M_2. (Pls 2, p. 97 and 7, p. 127.)

Isolated teeth. M 14082, right M^1; M 16381, right dp_4; M 18788, right I^1; M 32230, right C; M 32231, left P^3; M 32232, left C; M 32233, left C; M 32234, right P_3; M 32237, left P^3; M 32238, left C; the remaining specimens are listed in Tables 1–22.

DESCRIPTION. The following description is based entirely on the specimens from Rusinga and Mfwangano Islands. The Songhor specimens are divergent in a number of characters, and this probably signifies a taxonomic difference which will be commented on after the description.

Maxilla and premaxilla (Table 1, p. 134–5). The premaxilla is a relatively small bone. The nasal processes are not complete on any specimen, but it appears from the convergence of the maxillo-premaxillary suture with the lateral margin of the nasal cavity that they extend no further than two-thirds of the way up the nasal aperture. Alveolar procumbency appears well developed, but only a single female individual is measurable: naso-alv. ht is 6·1 mm and the index (naso-alv. ht/ M^1–M^3) × 100 is 32·5%. The incisor roots are inclined anteriorly, and this, in combination with a short true diastema of 2·3 mm, produces a much larger functional diastema similar to that of modern apes.

The nasal aperture appears to have been narrow, reaching a maximum breadth on RU 1850 of only 12 mm. The floor of the aperture is a narrow gutter, uncomplicated by any grooves posteriorly. After having been divided in two by the nasal septum, the floor of the nasal cavity continues at a constant width of 11 mm in RU 1849, and an estimated 12 mm in RU 1774.

The alveolar process of the maxilla is fairly shallow. It is mainly occupied by the maxillary sinus, which is very large. The anterior wall of the sinus is above P^3, and it extends posteriorly into the tuberosities of the alveolar process beyond M^3. The floor of the sinus extends into the widely-flaring zygomatic process on the right side of RU 1774, and on all the specimens it penetrates down into the spaces between the roots of the molars so that the ends of the roots, with a thin bony covering, penetrate up into the sinus. The tuberosities of the alveolar process on specimen RU 1850 are very small and rounded, extending no more than 2 mm beyond M^3. On RU 1774, on the other hand, the tuberosity on the intact side is prolonged posteriorly into an angular process nearly 7 mm beyond M^3. The maxillary sinus extends into this process. The greater palatine foramen enters the palate posterior to M^3 in this specimen, but in RU 1850 it enters opposite the mesial border of M^3.

The zygomatic process of the maxilla is above M^2 in both specimens, but whereas in RU 1850 the height of the process above the base of the crown of M^2 must have been at least 6 mm, in RU 1774 it is only 2·4 mm. Since these are both adult female individuals, the feature is evidently extremely variable in this species.

The palate is not preserved intact on any specimen, although much of it is preserved on RU 1850. It is relatively long and narrow, and the indices for breadth over length are all less than 50%. The tooth rows diverge slightly from P^3 to M^3, and the index of breadth at M^2 over breadth at C is 106%.

Mandible (Table 2, p. 136–7). The mandibular symphysis is extensive and well buttressed. It is fairly deep, and the index of (t/d) × 100 for five individuals is 46%. There is a well-developed superior transverse torus about one-third of the way from the inferior border. Above this the lingual border of the symphysis runs straight to the incisor alveolus, while below it the border is moderately concave due to development of the genial fossa. This is shallow and on most specimens lacks any tubercle development. The inferior border of the symphysis is sharply rounded and an inferior transverse torus is usually present. Where the inferior torus is well developed the most posterior part of the symphysis is usually at the inferior border. The buccal border of the symphysis is gently and evenly convex from the inferior border to the incisor alveolus.

Posterior to the symphysis the body of the mandible gets shallower. The depth of the body at M_2 is 73% of the symphyseal depth, but the robusticity of the body remains very similar to that of the symphysis. The type mandible, described by Clark & Leakey (1951 : 76), gives a misleading picture of the construction of the mandibular body owing partly to the crushing to which this specimen has been subjected and partly to its unusually gracile construction. Most other specimens are considerably more robust than the type specimen. There is a single mental foramen about one-third of the way up from the inferior border of the mandible. The line of attachment of the buccinator muscle lining the outside wall of the buccal cavity is prominent and follows the usual hominoid pattern. Medially, the mylohyoid line is not easily seen except on one specimen (RU 1857), and again follows the usual pattern.

The mandibular ramus is not preserved on any specimen. The root of the ramus arises opposite

M_3 and overlaps the distal quarter of it. The pterygoid fossa is incompletely preserved on two specimens and appears very deep. The thickness of bone posterior to M_3 decreases sharply so that at the pterygoid fossa it is extremely thin but with a thickened buttress running along the inferior border. In addition, the inferior border starts to swing out inferiorly, posterior to the level of M_3, and this could indicate that the angle of the mandible was inflated.

Upper incisors (Tables 3–4, p. 138–140). The I^1 is a slim high-crowned spatulate tooth. The crown is usually asymmetrical with the distal border convex and the highest point of the crown at the mesial end of the incisive edge. The latter is appreciably shorter than the greatest mesiodistal length. The lingual surface is gently concave and usually has only the slightest trace of a lingual pillar. The cingulum is small and usually no lingual tubercle is developed. The buccal surface is convex and unmarked. The crown is worn along its incisive edge and down the lingual surface, abrasion of the latter having the effect of keeping the incisive edge always sharp. The I^1 of the Songhor population is much broader and more spatulate.

The I^2 is high-crowned like the I^1 and has a pointed apex. The incisive surface is that part mesial to the apex of the crown. The mesiodistal length is much reduced in comparison with the I^1. The lingual surface is simple, gently convex, and lacking any trace of lingual tubercle or pillar. The crown thus appears spatulate when unworn, but the effects of wear drastically alters this; the incisive surface is worn down, sharpening the tip of the crown into a dagger-like point, and the distolingual surface develops a deep wear notch from wear against the lower C. In these conditions it is not always easy to distinguish the worn I^2 from a small canine. (See Fig. 6.)

Upper canine (Table 5, p. 141–3). The upper canines show marked variation in both morphology and size. The large teeth, which are associated with molars in three specimens, are extremely characteristic of this species and are different from all other hominoids known. The large (presumably male) upper canine is a blade-like tooth deeply furrowed by grooves. The mesial ridge is very prominent and has a deep groove on either side of it; one is the mesial groove normally found on the lingual margin of the ridge, while the other is on the buccal margin. (The mesial ridge is identified from the origin of the lingual cingulum at its base.) Distal to the grooves both surfaces of the crown are slightly concave, the lingual face more so than the buccal. The two faces meet at the distal ridge which is narrow and prolonged into a knife-like flange. The lingual face of the crown is marked by numerous striations, while yet another shallow groove is typically present midway across the buccal face. The lingual cingulum is small and broken up by the vertical striations of the lingual surface. It is largest mesially and becomes smaller distally, usually not reaching the distal ridge. The wear on these large canines is characteristically distolingual, cutting across the lingual face of the distal flange-like ridge. There is also a flat wear facet developed mesially across the lingual mesial groove of the upper canine, made by the action of the lower canine. (See Fig. 6.)

The smaller (female) canines also have a knife-like appearance but the mesial ridge and single mesial groove are only moderately developed. The buccal surface is convex and not marked by any groove, and the lingual surface is only slightly striated and is flat rather than concave. The distal ridge is still pronounced, but it is not extended distally as in the larger teeth. The cingulum is slightly better developed and continues all the way to the distal ridge. The range of variation of the upper canine is extremely large, far greater than is seen in any other comparable-sized primate. This is reflected in the high values for standard deviation and coefficient of variation. The breadth/length index is low on both large and small teeth.

The Songhor population has canines as large as or larger than the Rusinga one. Some of the large ones, however, lack the double mesial groove and are less bilaterally compressed and more tusk-like.

Upper premolars (Tables 6–7, p. 144–6). The P^3 is a specialized tooth as part of the sectorial complex. The buccal cusp is much larger than the lingual one, and it is bilaterally compressed

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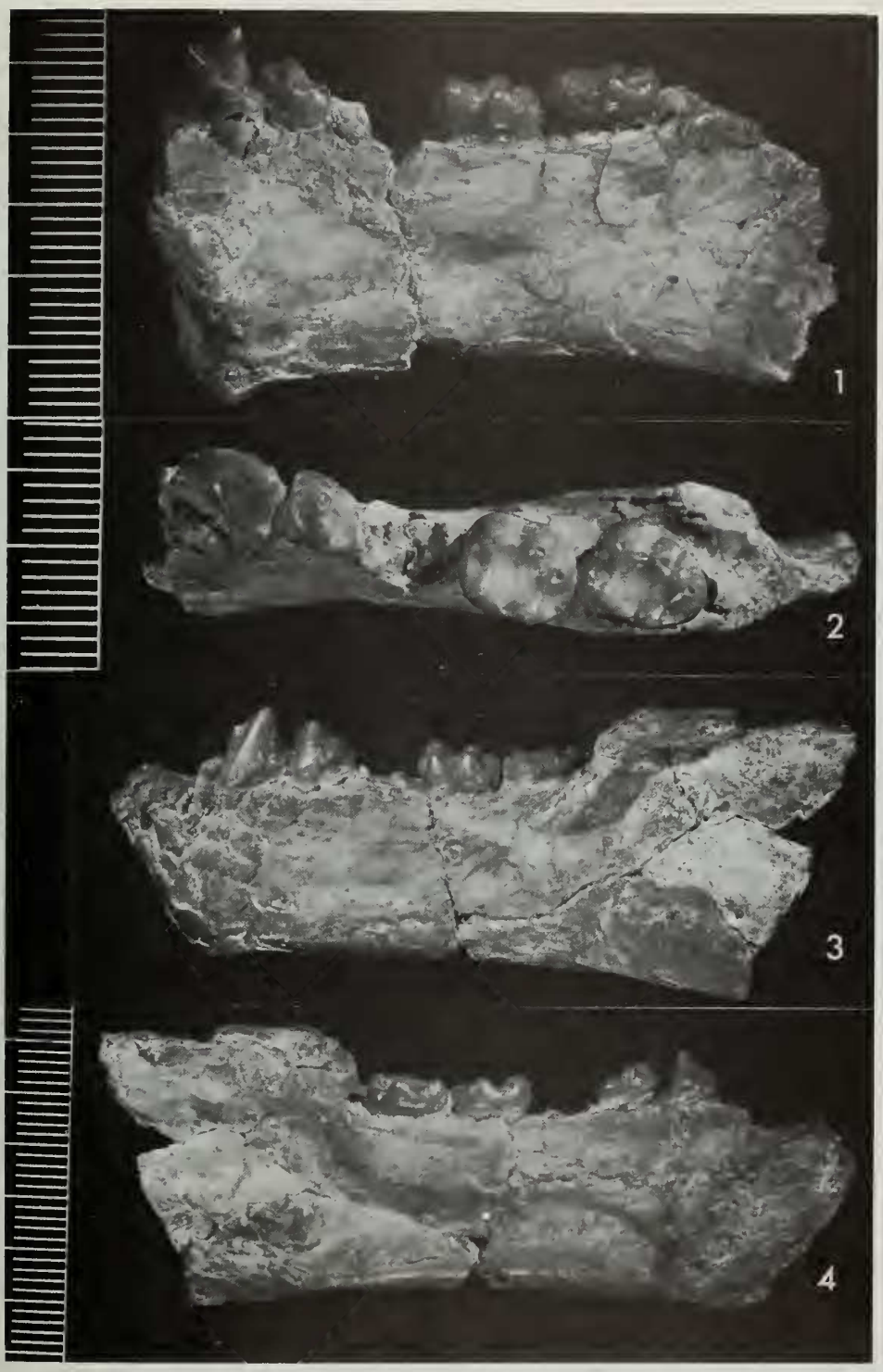
Plate 7

Figs 1–4 *Dendropithecus macinnesi* (M 16650). Figs 1–2, right mandible, lingual and occlusal views. Figs 3–4, left mandible, buccal and lingual views.


1
2
3
4

with sharp ridges running mesially and distally. The mesial ridge occludes against the back of the single-cusped P_3 and the distal ridge against the buccal cusp of P_4. The mesiodistal length is greater at the level of the buccal cusp than at the lingual cusp. In overall shape the P^3 is mesiodistally compressed with a higher breadth/length ratio than P^4. The morphology of the occlusal surface is simple. There is at least one transverse ridge, and in one specimen two, but this does not reach the tip of either cusp. The lingual cusp is skewed mesially relative to the buccal one and is set directly on the mesial border of the tooth. There may be a slight mesial cingulum, but the lingual cingulum is completely lacking and only the distal cingulum is at all well developed.

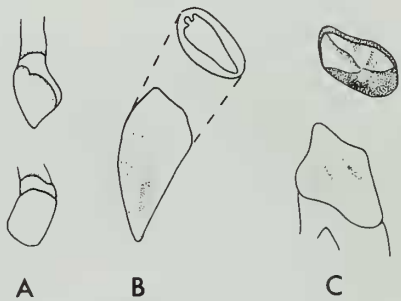


Fig. 6 Anterior teeth of *Dendropithecus macinnesi*, × 1. A, lingual and buccal views of I^2. B, lingual view and cross-section of large male canine crown. C, buccal and occlusal view of P_3.

The P^4 is the same size as the P^3 but lacks its buccal elongation and projecting buccal cusp. The mesiodistal length is slightly greater, so that the buccolingual breadth being the same, the breadth/length ratio is lower. Two transverse ridges are developed on the occlusal surface. There is a very slight mesial fovea cut off by the first of these ridges. The cingulum is strongly developed on the lingual and distal edges of the P^4 and runs from the mesial border of the lingual cusp to the distal border of the buccal one, where it forms a slight tubercle on the distobuccal corner.

The P^3 and P^4 of the Songhor population are relatively very small compared with the Rusinga sample. They are much less sectorially specialized and in fact are remarkably similar to the premolars of *L. legetet*.

Upper molars (Tables 8–10, p. 147–153). The M^1 is a symmetrical tooth, the four cusps being nearly equal in size and only the hypocone differing by being slightly smaller. The crown is always broader than long, more so than is usually found for second and third molars, which are both larger and more elongated than the first. The occlusal surface is crossed by a number of very well-defined ridges. The mesiobuccal ridge of the protocone is a robust but short ridge and divides into two at the base of the protocone. The resulting two ridges would appear to be homologous with the mesial and distal ridges of the protoconule (Korenhof 1960) and the point of division homologous with the protoconule itself, but this cusp is never developed in this species. The distal ridge of the protoconule runs directly buccally to the tip of the paracone. Bounded distally by these ridges, and mesially by the mesial marginal ridge of the tooth and a short mesial ridge from the paracone, is a narrow mesial fovea. This is limited to the buccal half of the crown by the conformation of the ridges; functionally, it constitutes part of an occlusal basin the mesial part of which is continued by the distal cingulum of the P^4.

The distobuccal ridge of the protocone, or crista obliqua, is also well defined. It connects the protocone and metacone, usually without a break. Together with the distal ridge of the protoconule, just described, it delimits the trigon basin which is completed buccally by the rather cristodont formation of the paracone and metacone. The ridges of the hypocone are variously developed, but there are commonly two, neither as well defined as the preceding ridges. There is a ridge running mesially to the distal border of the protocone, and another running buccally to the base of the metacone, sometimes almost reaching the tip of this cusp.

The lingual cingulum is strongly developed. Mesially it runs from the end of the mesial ridge

of the protocone, encircles the protocone, and continues without a break onto the lingual border of the hypocone. At the distolingual corner of the hypocone there is a break and there is a short distance without any cingulum until the start of the distal cingulum. This is a broad shelf forming the distal part of the tooth beyond the buccal ridge of the hypocone. Where it connects with the metacone a small tubercle may be developed distobuccally on this cusp. A similar tubercle may be present on the mesiobuccal corner of the paracone where the mesial marginal ridge impinges on it, and in view of this similarity it is possible that the mesial fovea originates partly from the mesial cingulum. There is also a small buccal cingulum developed in the gap between paracone and metacone.

The M^2 is extremely similar to the M^1, differing only in being larger and in having more distinct occlusal ridges and cingula. The crown is more oblique due to the reduction in size of the metacone. The greatest buccolingual breadth is therefore across the paracone–protocone. The lingual cingulum is sometimes continuous with the distal cingulum around the base of the hypocone.

The morphology of the M^3 is again very similar to that of M^1. The metacone and hypocone are both much reduced, but usually present, so that the tooth is often triangular, the apex being at the distal end. The protocone is very much the largest cusp and the lingual cingulum is massive. Despite the reduction distally, the M^3 is still larger than M^1 and is still relatively longer.

Lower incisors (Tables 11–12, p. 154–5). The I_1 is high-crowned and symmetrical. The morphology is simple; the lingual face is concave and lacks any trace of a cingulum, and the buccal face is convex. The I_2 crown is strongly asymmetrical, the mesial edge being concave and the distal edge convex. This curvature is continued in the root, so that the whole tooth is curved, especially so in the Songhor specimens. The lingual face of the crown is simple, unmarked by any ridges, and has only the slightest trace of a cingulum at the base of the crown.

Lower canine (Table 13, p. 156–8). In morphology the lower C is very like that of *Limnopithecus legetet*, and in size they overlap considerably. Hence it is difficult to assign small canines to either species. Those specimens from Rusinga Island, of the same size and with similar indices to RU 1850, I have arbitrarily assigned to *Dendropithecus macinnesi*, leaving only a few very small specimens from Rusinga with *L. legetet*. The position for Songhor is more difficult; the large canines fairly clearly belong to *Dendropithecus macinnesi*, but the smaller ones, which could be of either, I have assumed are more likely to belong to *L. legetet* because at Songhor this species is much more common than *D. macinnesi*. The errors introduced by this approach are not likely to be great. They are that the frequency proportion of *L. legetet* to *D. macinnesi* at Songhor may be slightly weighted in favour of the former, and that the means for the lower canine dimensions of the latter may be slightly biased in favour of the larger specimens.

The crown of the C is slender and slightly distally curved. The breadth/length index is low. The only ridge well developed is the mesial one, which is short, and the base of the crown curves up mesially to meet it. There is no cingulum. During wear, a deep notch may be cut buccodistally by the upper canine on both male and female individuals.

Lower premolars (Tables 14–15, p. 159–162). The P_3 is a highly specialized tooth, almost caniniform and strongly sectorial. It is strongly bilaterally compressed, has a single acutely pointed cusp, and is set sharply obliquely from the axis of the molar series. The breadth/length index is very low. The enamel extends far down the cervical border of the mesial root, and with wear a flattened elongated wear facet develops on the mesiobuccal surface. The mesial extension of the enamel is shown by the index (distal ht/mesial ht) × 100 in Table 14. (See Fig. 6.)

The ridges are well developed. The mesial ridge is particularly prominent, and in M 16650 it has a distinct tubercle at its junction with the lingual cingulum not present in the other specimens. The mesial ridge meets the cingulum at its highest point along the crown. The lingual ridge is also well developed, and between these two ridges and the cingulum the lingual surface of the tooth is distinctly concave. The junction of the lingual ridge with the cingulum varies from a perfect junction at an elevation of the cingulum to an incomplete junction at a low and diffuse elevation. The distal ridge is less well developed than the others. Between it and the lingual ridge the surface is again deeply concave, and passes down onto a small basal talonid. The degree of excavation of the talonid depends on degree of wear, the lingual cusp of the P^3 occluding on this surface.

The P_3 of the Songhor specimens is more robust and probably less specialized sectorially. It is a very big tooth, correlated with the large canines of this subspecies. By contrast the P_4 is very much smaller.

The P_4 is a highly specialized tooth, more a part of the sectorial complex than of the molar row. It has two main cusps arranged perpendicular to the line of the molars, but the long axis of the tooth is set obliquely to this, at a somewhat smaller angle than the P_3, so that the mesio-distal length is only 80–90% of the maximum length. As in the P_3 the enamel is extended down the cervical border of the mesial root. The crown is longer than broad. The buccal cusp is more strongly developed than the lingual cusp. It is always greater in bulk and in some specimens it is considerably higher as well. The two cusps are joined by a well-defined transverse ridge. The buccal cingulum is only slightly developed mesially, but increases distally. It starts mesially at the end of the mesial buccal ridge and descends almost vertically to below the buccal cusp. It then starts to ascend slightly and increase in size until it ends prominently in the distobuccal tubercle. A small distal cingulum is developed between two distal tubercles.

Lower molars (Tables 16–18, p. 163–170). The M_1 is an oval-shaped tooth with rounded corners. It is slightly broader distally than mesially. All the cusps are interconnected by a well-developed ridge system. The protoconid is slightly in advance of the metaconid and is joined to it by a fairly high and distinct ridge, the distal trigonid ridge, which forms a prominent boundary between the trigonid and the talonid basins. The former is small and is bounded mesially by a low and poorly-developed ridge, the mesial trigonid ridge. It is relatively shallow and set well above the level of the talonid basin. The trigonid as a whole is constricted in this tooth. The talonid ridges are mostly well developed, and the talonid basin therefore appears completely encircled by ridges, except for the lingual border which opens in a broad and deep V-shaped depression between the metaconid and the entoconid. The size of the talonid basin is somewhat constricted, however, by the medial position of the hypoconulid which occupies the distal part of the talonid basin. The cingulum is relatively more strongly developed in M_1 than on the other molars. It starts at the mesial ridge of the protoconid, increasing to the buccal border of the protoconid where it is large and shelf-like. It is continuous around the hypoconid and ends at the buccal border of the hypoconulid.

The M_1 in the Songhor population is smaller and less elongated than that of the typical Rusinga subspecies. This is quite a striking difference and casts doubt on their inclusion in one species, and will be discussed in more detail in the next section, p. 131.

The M_2 is much larger and squarer than M_1. The protoconid is level with the metaconid and the two cusps are widely separated. The mesial trigonid ridge is not developed, but the distal trigonid ridge is prominent and cut by a longitudinal valley. The trigonid basin is large and broad, because the protoconid is widely separated from the metaconid, and it is fairly shallow. The distal ridges of the protoconid and the hypoconid are not developed, and deep grooves pass between these cusps. The entoconid–hypoconulid ridge is low but well defined with a large distal fovea behind it, also worn by the hypocone of the M^2. The talonid basin is large, broad and shallow, partly the result of the more buccally placed hypoconulid. The buccal cingulum is less distinct and is slightly cut by the buccal main groove; it is very small on the protoconid, reaching its maximum development in the interval between the protoconid and the hypoconid.

The M_3 is the largest tooth in the molar series. It is similar to M_2 except that the hypoconulid is extremely buccally displaced, being about in line with the other buccal cusps, and the cingulum is slightly more distinct. Ridge development is the same as in M_2.

Deciduous dentition (Tables 19–21, p. 171–3). The di^2 are high-crowned caniniform teeth, strongly mesiodistally compressed. There is a moderately long incisive edge mesial to a sharp lingual crest. The lingual crest arises from a rather small lingual pillar, which in turn arises from the massive shelf-like lingual cingulum. One of the specimens has a distal wear notch near the tip of the crown, indicating the cutting action of the lower deciduous canine.

The crown of the upper dc is relatively high compared with maximum length. It is rather featureless except for sharp mesial and distal ridges, giving it the blade-like appearance of the permanent canine, and shelf-like lingual cingulum.

The dp^4 is typically molariform, very like M^1. It is only the small size, the thinness of the

enamel, and the splayed roots that suggest the two isolated specimens are milk teeth of this species.

The lower dc is very like the permanent lower canine. It is relatively high-crowned for a milk tooth, and has the short mesial ridge characteristic of canines. The lingual cingulum is more strongly developed, however, and the enamel is thin.

The dp_4 is an extremely elongated tooth. The protoconid–entoconid ridge is strongly oblique and the trigonid is elongated and narrow. The talonid ridges are prominent, encircling the very large talonid basin. The cingulum is hardly developed at all. This tooth is strikingly different from the dp_4 of *Limnopithecus legetet* and is equally different from that of other dryopithecines.

REMARKS. This species shows such a remarkable degree of variation that it is difficult to know how to handle it taxonomically. The population from Rusinga and Mfwangano Islands show a higher degree of sexual dimorphism than any other primate I am familiar with, including baboons and gorillas, and the many differences of the Songhor specimens increases that variability still further. Because of the coherent nature of the Rusinga and Mfwangano samples they clearly belong together, but some degree of differentiation appears to be recognizable in the Songhor sample. This is attributed here to a subspecies difference based on the combination of broader and more spatulate incisors in the Songhor sample, more tusk-like canines, larger and more robust P_3, shorter and broader P_4 and M_1–M_3, smaller upper premolars and molars, and deeper mandibular bodies.

Dendropithecus macinnesi macinnesi (Le Gros Clark & Leakey 1950)

TYPE AND DIAGNOSIS. As for species.

LOCALITY AND HORIZON. The Lower Miocene of Rusinga and Mfwangano Islands, and Karungu, Kenya.

Dendropithecus macinnesi songhorensis subsp. nov.

1943 *Limnopithecus legetet* Hopwood; MacInnes: 151.

DIAGNOSIS. A subspecies of *D. macinnesi* distinguished from the type subspecies by the following features: I^1 relatively broader, less high-crowned and more spatulate; I^2 by contrast relatively small; C less bilaterally flattened, large and tusk-like; upper premolars and molars similar in morphology but much smaller, and the M^3 cusps, though reduced in size, all well developed; P_3 less bilaterally flattened with less enamel extension onto the mesial root, very large and robust; P_4 similar in morphology but much smaller; M_1 with relatively large buccal cingulum, oblique transverse ridges (protoconid is mesial to metaconid and hypoconid to entoconid), and the hypoconulid medially placed. I^1, Cs and P_3 are all relatively very large compared with the molars and P4. The mandible is deep and less robust than the type subspecies.

HOLOTYPE. KNM-SO 378, right mandible with the crowns of P_4–M_3 well preserved.

LOCALITY AND HORIZON. The Lower Miocene of Songhor and Koru, Kenya.

MATERIAL. 31 specimens. M 14083 mandible and symphysis with left P_3; KNM-SO 378 mandible with right P_4–M_3; SO 405 symphysis with right C; SO 530 mandible with right P_3 and M_1–M_2; SO 539 maxilla with left I^1–P^4. M 14082, right M^1, and M 18788, right I^1, are provisionally assigned to this subspecies, as are all of the Songhor specimens listed as *D. macinnesi* in Tables 1–21.

HOMINOIDEA INDETERMINATE

There are a number of specimens which cannot satisfactorily be placed into any of the extant hominoid species from the East African Lower Miocene. These specimens are too fragmentary to be named, or for their affinities to be assessed, so all that can be done here is to place them on record by means of brief descriptions.

M 32309 (Chianda Uyoma, collected by W. E. Owen in October 1935). It is a left upper C with the crown and much of the root intact and well preserved. The crown is low-crowned and has a peg-like appearance as a result of its massive lingual cingulum development. The mesial groove is broad and shallow, the distal ridge is small, and both are dwarfed by the shelf-like lingual cingulum which connects them without a break. The tip of the crown is worn almost flat, and the facet continues distally onto the much narrower distal wear facet. Mesially there are faint traces of wear on either side of the mesial groove. Dimensions of this tooth are: maximum length 7·9 mm, perpendicular breadth 6·0 mm, buccal height 9·1 mm. This specimen was found by Mr C. Madden in the BM(NH) collections.

KNM-LS 1 (Losidok 1 : 1951). Described by Clark (1952 : 276) as *P. africanus*. This specimen is a right lower C, well preserved but moderately worn; the extreme tips of root and crown are broken. Its dimensions are: maximum length 8·7 mm, perpendicular breadth 5·4 mm; index (b/l) × 100 is 62·1 %. It is slightly smaller than most *P. africanus* canines and is considerably more strongly bilaterally compressed. Crown and root have a marked buccodistal curvature, enhanced by the short mesial ridge. The lingual cingulum is prominent. The crown is moderately worn with a well-developed distobuccal wear facet cutting into the top of the root.

KNM-MO 1 (Moruorot 1 : 1951). This specimen is a left mandible fragment with M_3 and roots of M_1–M_2. It is weathered and part of the bone cortex is missing on the medial surface of the body. M_3 is weathered and most of the enamel is missing on the lingual edge of the crown. Mandibular dimensions at M_2 are: depth 17·8 mm, thickness 10·5 mm; index (t/d) × 100 is 58·6 %. M_3 dimensions are: md 9·2 mm, bl mes 7·3 mm, bl dist 6·7 mm; bl/md is 79·4 %. A very approximate estimate of M_1–M_3 length is 25 mm. The size of both mandible and teeth is small for *P. africanus*, although the morphology of M_3 is almost certainly pongid rather than hylobatid. The M_3 was apparently only slightly bigger than M_2.

KNM-SO 1236 (Songhor 760 : 1972). This specimen was found with SO 1237 at an exposure of red beds in the Mtete Valley near Songhor. It is a mandible fragment with the symphysis and part of the left body with root of C and root sockets of all the incisors and left P_3–P_4. The body and symphysis are broken inferiorly but the depth was probably not greater than 18 mm. The thickness at the symphysis is 14·7 mm, giving a high index of 81·7 %. The central incisor roots are much shorter buccolingually than the lateral incisors (approximately $\frac{2}{3}$ the length). The canine root dimensions are 10·0 mm for length and 6·0 mm for breadth, giving an index of 60 % comparable to the value for KNM-LS 1.

KNM-SO 1237 (Songhor 761 : 1972). This specimen is a right upper C, weathered but intact. The tip of the root is broken. The crown is moderately worn, with a flat facet across the tip passing into a facet down the distal edge narrowing towards the base of the crown. In this and in its general morphology this specimen from Songhor is almost identical to M 32309 from Chianda Uyoma. The dimensions are 8·4 mm for length and 6·3 mm for breadth, giving an index of 75 %. The lingual cingulum is very prominent on this specimen. This and KNM-SO 1236 were found within 2 ft of each other and at the same level, and it is likely that they go together, especially as no other primate specimens were found at this locality.

Measurements, univariate statistics, and bivariate plots

Tables of measurement

Tables 1–22 give dimensions of all cranial material of Kenya fossil apes. Each table covers just one body part; for instance there is a separate table for the maxilla, the mandible and for each tooth in the dentition. Within each table there are subdivisions by species with the specimens listed singly. In Tables 3–18, which cover the main part of the collection, the specimen dimensions are followed by sample statistics: the mean, the number of specimens, the standard deviation, the coefficient of variation, the standard error, and the 95% confidence limits of the sample (the last few parameters were not calculated on small samples). Index ratios are given as percentages in every case.

Table 1 Maxillary measurements.

	D. macinnesi KNM-RU 1774	1799	1849	1850	1901	2986	*P. (R.) gordoni* KNM-SO 401	700	*P. (R.) vancouveringi* KNM-RU 2058
naso-alv. ht	–	–	–	6·1	–	–	–	10·0	–
ht/M^1–M^3	–	–	–	32·5	–	–	–	35·0	–
nasal aperture									
ht	–	–	–	–	–	–	–	21·0	–
b	–	–	–	12·0	–	–	–	15·4	–
b/ht	–	–	–	–	–	–	–	73·3	–
zyg. arch									
position	–	M^2	–	M^2	–	M^2	M^1	M^1	M^2
ht	–	2·4	–	6·0	–	8·0	3·5	4·7	4·3
max. sinus									
L	–	26·6	–	23·8	–	–	–	31·0	18·7
B	–	14·0	–	11·5	–	–	–	14·0	15·0
B/L	–	52·6	–	48·3	–	–	–	46·7	80·0
pal. b at M^2 (ext)	–	–	–	31·7	–	–	–	39·2	–
B/pal b at M^2 (ext)	–	–	–	36·3	–	–	–	37·0	–
palate									
L	–	–	–	35·0	–	–	–	53·4	–
B at C	–	–	–	14·9	–	–	–	21·4	–
M^2	–	–	–	15·4	–	–	–	22·0	–
B at C/M^2	–	–	–	96·8	–	–	–	97·0	–
B at M^2/L	–	–	–	44·1	–	–	–	41·3	–
depth at C–P^3	–	–	–	2·6	–	–	–	2·5	–
M^2	–	–	–	4·3	–	–	–	5·4	–
M^1–M^3	18·6	16·5	19·6	19·0	20·0	27·7	–	28·6	22·5
P^3–M^3	27·6	–	29·1	27·0	–	–	–	39·6	–
C–M^3	33·7	–	–	33·8	–	–	–	51·0	–

L. legetet KNM-SO 421 535	443	537 538	*P. africanus* M 14084	KNM-RU 1705 2036	1792	M 32363	*P. nyanzae* KNM-RU 1965 M 16647	1674	1677	*P. major* M 16649	UM-P 62-11
4·6	5·2	5·9	–	11·0	10·1	11·1	16·0	–	–	–	16·7
–	–	–	–	–	–	41·5	–	–	–	–	45·5
–	–	–	–	–	–	23·0	37·0	–	–	–	36·0
–	–	–	–	–	–	14·0	19·0	–	–	–	30·2
–	–	–	–	–	–	60·8	51·4	–	–	–	84·0
M^2	M^2	M^2	$M^{1/2}$	M^1	$M^{1/2}$	M^2	M^2	M^2	M^2	M^1	M^2
5·6	4·0	4·0	10·4	6·0	–	7·1	17·0	14·0	12·0	11·0	14·0
–	–	–	–	–	–	–	–	32·0	–	–	46·0
7·5	7·4	6·0	–	10·5	–	11·2	–	–	19·0	18·0	17·0
–	–	–	–	–	–	–	–	–	–	–	37·0
–	–	–	–	–	–	–	59·0	–	–	–	61·0
–	–	–	–	–	–	–	–	–	–	–	28·0
–	–	–	51·0	–	–	45·0	66·0	–	–	–	79·0
–	–	–	–	–	–	19·0	30·5	–	–	–	37·0
–	–	–	26·0	–	–	23·6	32·0	–	–	–	34·4
–	–	–	–	–	–	42·2	95·5	–	–	–	108·6
–	–	–	51·0	–	–	52·4	48·5	–	–	–	43·6
–	–	–	4·0	–	4·7	5·1	7·0	–	–	–	4·0
–	–	–	5·9	–	6·1	6·8	10·2	–	–	–	7·5
–	–	–	25·0	–	–	25·8	33·2	28·4	33·2	–	36·7
–	–	–	38·1	–	–	36·5	46·8	41·5	48·5	–	54·6
–	–	–	49·5	–	–	44·4	61·9	–	–	–	73·7

Table 2 Mandibular measurements.

		symphysis			body at P_4			body at M_2			M_2 d / symph d	M_2 d / P_4 d	M_1–M_3	P_3–M_3	C–M_3	I–I	C–C	P_4–P_4	M_3–M_3
		d	t	t/d	d	t	t/d	d	t	t/d									
D. macinnesi																			
RU	900	23·9	10·1	42·3	18·1	6·7	37·0	16·0	8·6	53·7	66·9	88·4	–	–	–	–	–	–	–
	1726	–	–	–	–	–	–	15·6	7·9	50·7	–	–	23·0	–	–	–	–	–	–
	1727	–	–	–	16·8	7·7	45·8	–	–	–	–	–	–	–	–	–	–	–	–
	1844	–	–	–	–	–	–	16·3	7·3	44·8	–	–	–	–	–	–	–	–	–
	1850	–	–	–	15·4	7·7	50·0	14·1	8·2	58·2	–	91·5	20·2	29·5	35·7	–	–	–	–
	1857	21·1	11·2	53·1	17·3	8·2	47·4	15·6	8·4	53·9	74·0	90·2	22·9	34·5	41·8	–	–	–	–
	1901	–	–	–	–	–	–	17·0	8·5	50·0	–	–	22·0	–	–	–	–	–	–
	2001	22·2	9·5	42·7	15·4	6·7	43·5	–	–	–	–	–	–	–	–	–	–	–	–
	2015	22·5	10·3	45·8	19·0	9·0	47·4	17·3	9·1	52·6	77·0	91·0	23·5	34·8	41·4	–	–	–	–
M	16650	–	–	–	18·6	7·3	39·3	17·8	7·8	43·8	–	95·8	21·6	34·3	41·6	–	–	–	–
MW	51	17·1	8·0	46·8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	53	–	9·6	–	17·4	7·6	43·7	16·6	7·0	42·2	–	95·4	–	–	–	–	–	–	–
Mean		21·4	9·8	46	17·3	7·6	44	16·3	8·1	50	73	93	22·2	33·3	40·1	–	–	–	–
Number		5	6	5	8	8	8	9	9	9	3	6	6	4	4	–	–	–	–
P. (R.) gordoni																			
SO	463	–	–	–	27·0	10·2	37·8	25·0	11·6	46·4	–	88·0	29·0	–	–	–	–	–	–
	464	–	–	–	–	–	–	16·1	10·5	65·2	–	–	–	–	–	–	–	–	–
	1112	33·2	18·5	55·7	29·7	12·0	40·4	25·7	14·5	56·4	77·0	86·0	28·3	43·5	64·3	–	–	–	–
Mean		33·2	18·5	56	28·4	11·1	39	22·3	12·2	56	77	87	28·7	43·5	64·3	–	–	–	–
Number		1	1	1	2	2	2	3	3	3	1	2	2	1	1	–	–	–	–
L. legetet																			
SO	376	16·0	7·4	46·3	14·7	6·4	43·6	13·6	5·4	39·8	84·9	92·6	–	–	–	–	–	–	–
	385	–	–	–	14·4	6·2	43·0	15·0	6·3	42·0	–	107·0	18·5	27·5	–	–	–	–	–
	386	21·4	7·8	36·5	16·4	7·2	43·9	15·3	8·1	52·9	71·6	93·3	18·3	27·5	33·8	11·0	9·6	17·4	–
	387	–	–	–	–	–	–	16·2	7·8	48·2	–	–	21·7	–	–	–	–	–	–
	388	–	–	–	–	–	–	17·8	8·1	45·5	–	–	–	–	–	–	–	–	–
	452	17·0	7·4	43·5	14·3	5·9	41·3	–	–	–	–	–	–	–	–	–	–	–	–
	481	–	–	–	–	–	–	16·4	8·3	50·6	–	–	–	–	–	–	–	–	–
	533	17·4	7·5	43·1	14·0	6·0	42·9	–	–	–	–	–	–	–	–	–	–	–	–
	534	–	–	–	–	–	–	12·8	6·2	48·4	–	–	–	–	–	–	–	–	–

Mean	17·4	7·5	43	14·8	6·4	43	15·1	7·2	48	82	97	19·1	27·3	33·3	11·0	9·6	17·4	–
Number	7	7	7	6	6	6	8	8	8	3	4	4	3	2	2	1	1	–
P. africanus																		
M 32363	30·0	12·0	40·0	22·2	10·1	45·5	19·3	11·9	61·6	64·4	87·0	30·0	43·3	50·8	–	–	–	–
RU 1680	–	–	–	23·0	10·1	43·9	22·4	9·7	43·3	–	97·5	–	–	–	–	–	–	–
1706	–	–	–	–	–	–	–	–	–	–	–	29·4	42·3	49·3	–	10·2	18·3	–
1728	27·0	11·6	43·0	23·1	10·7	46·3	21·0	11·9	56·6	77·7	91·0	25·2	36·5	43·3	–	–	–	–
1855	26·7	12·2	45·8	20·8	11·0	52·9	19·8	11·5	58·1	74·6	95·2	27·2	40·0	48·0	13·5	13·8	22·1	31·3
1864	24·6	11·4	46·3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1955	23·6	11·5	48·7	19·6	10·2	52·0	20·1	11·7	58·2	85·2	102·6	–	–	–	–	–	–	–
2036	24·0	11·8	49·2	19·2	9·8	51·0	18·4	12·3	66·8	76·7	95·9	29·6	43·4	51·2	–	15·4	16·9	20·4
SO 372	27·5	12·8	46·5	22·0	9·7	44·1	–	–	–	–	–	–	–	–	–	–	14·2	21·4
391	–	–	–	–	–	–	17·3	10·2	59·0	–	–	–	–	–	–	–	–	–
Mean	26·2	11·9	46	21·4	10·2	48	19·8	11·3	58	76	95	28·3	39·1	48·5	13·5	13·8	20·7	31·3
Number	7	7	7	6	6	6	6	6	6	5	6	6	6	6	1	3	4	3
P. nyanzae																		
RU 1674	40·2	17·5	43·6	31·9	14·4	45·2	32·8	16·3	49·7	81·8	102·9	31·3	44·7	57·5	21·0	19·0	27·0	32·4
1676	–	–	–	–	–	–	–	–	–	–	–	36·8	54·5	68·7	–	–	–	–
1678	–	–	–	28·0	14·4	51·4	24·7	14·7	59·5	–	88·3	33·5	48·1	–	–	–	–	–
1711	35·5	16·2	45·6	30·4	13·0	42·7	–	–	–	–	–	–	–	–	–	–	–	–
1740	40·0	18·0	45·0	37·0	14·0	37·8	–	–	–	–	–	–	–	–	–	–	–	–
1840	36·4	18·3	50·2	–	–	–	–	–	–	–	–	–	–	–	17·6	15·3	–	–
1947	38·5	19·3	50·2	30·7	11·8	38·4	28·5	14·7	51·6	76·1	92·9	35·0	53·1	66·7	–	–	–	–
1982	–	–	–	–	–	–	–	–	–	–	–	37·4	–	–	–	–	–	–
2087	39·1	17·5	44·8	33·2	13·6	40·0	29·0	14·9	51·4	74·2	87·4	31·7	47·5	59·3	21·0	20·2	30·0	37·9
Mean	38·3	17·8	47	31·9	13·5	42	28·8	15·2	53	77	93	34·3	48·0	63·1	19·9	18·2	28·5	35·2
Number	6	6	6	6	6	6	4	4	4	3	4	6	5	4	3	3	2	2
P. major																		
M 14086	41·3	22·1	53·5	36·2	15·6	43·1	34·9	14·8	42·4	84·6	96·5	35·3	53·0	66·0	–	–	–	–
16648	–	–	–	–	–	–	–	–	–	–	–	44·4	65·6	–	–	–	–	–
SO 396	52·4	29·1	55·6	40·5	19·8	48·9	35·5	20·9	58·9	67·8	87·7	41·4	66·0	78·0	15·5	20·2	33·0	–
404	39·4	22·5	57·1	33·2	17·2	51·8	29·3	19·2	65·5	74·4	88·2	33·5	53·2	63·6	–	19·4	25·2	31·1
Mean	44·4	24·1	55	36·6	17·5	48	33·2	18·3	55	75	90	38·7	59·5	69	15·5	19·8	29·1	31·1
Number	3	3	3	3	3	3	3	3	3	3	3	4	4	3	1	2	2	1

Table 3 Measurements of upper I1.

	md	bl	bl/md	md/incis	md/root	incis/md	root/md	buc ht	md/buc ht
D. macinnesi									
M 18788*	6·4	4·3	67·2	5·2	4·5	81·2	70·3	7·5	85·4
RU 1651	6·0	4·9	81·6	4·2	4·3	70·0	71·7	9·0	66·7
1798	4·7	3·9	83·0	–	2·8	–	59·6	6·1	77·0
1806	4·7	4·2	89·5	3·2	3·6	68·1	76·5	6·0	78·4
1849	5·0	4·2	84·0	3·3	3·7	66·0	74·0	7·3	68·5
1850	4·9	4·3	87·8	3·5	3·3	71·5	67·4	6·9	71·0
1858	5·1	4·2	82·4	4·5	3·2	88·2	62·8	6·7	76·1
1901	5·2	4·9	94·2	3·8	3·6	73·0	69·2	7·0	74·3
SO 380*	6·4	4·7	73·4	–	–	–	–	–	–
417*	6·6	4·7	71·2	5·8	4·5	87·9	68·2	7·4	89·2
453*	6·3	4·5	71·4	5·2	4·4	82·5	69·7	6·9	91·3
Mean	5·1	4·4	86	3·8	3·5	73	69	7·0	73
Number	7	7	7	6	7	6	7	7	7
P. (R.) gordoni									
RU 1833	8·4	5·8	69·0	6·6	5·9	78·6	70·2	10·2	82·4
SO 551	6·9	5·1	73·9	6·2	4·5	89·9	65·2	10·2	67·6
552	6·7	5·3	79·1	5·1	4·3	76·1	64·2	8·9	75·3
553	7·6	5·7	74·9	6·2	5·9	81·6	77·7	9·3	81·7
Mean	7·4	5·5	74	6·0	5·2	82	69	9·5	78
Number	4	4	4	4	4	4	4	4	4
L. legetet									
M 14332*	5·2	3·6	69·3	4·8	3·4	92·4	65·4	5·3	98·1
RU 1826	4·3	3·4	79·1	–	3·3	–	76·8	–	–
2075	4·4	3·8	86·3	–	3·1	–	70·5	–	–
SO 476	4·8	3·7	77·0	4·0	3·1	83·3	64·6	5·3	90·6
483	5·0	4·0	80·0	–	4·2	–	84·0	–	–
489	5·4	4·0	74·1	–	3·2	–	59·3	6·2	87·1
490	5·4	3·9	72·3	4·4	3·1	81·5	58·5	6·0	90·0
504	5·1	4·3	84·4	4·2	3·9	82·3	76·5	5·3	96·2
548	5·0	3·8	76·0	4·0	3·5	80·0	70·0	5·7	87·7
565	4·8	3·7	77·1	–	3·4	–	70·8	5·8	82·7
1085	5·1	3·7	72·6	–	3·9	–	76·5	5·5	92·7
Mean	4·9	3·8	78	4·2	3·5	82	71	5·7	90
Number	10	10	10	4	10	4	10	7	7
S.D.	0·37	0·28	4·69	–	0·40	–	8·15	–	–
Coef. var.	7·6	7·4	6·0	–	11·4	–	11·5	–	–
S.E.	0·12	0·09	1·48	–	0·13	–	2·58	–	–
95% conf.	4·1	3·2	67	–	2·6	–	53	–	–
limits	5·7	4·4	89	–	4·4	–	89	–	–

*Not included in calculation of sample parameters.

Table 3 (*cont.*)

	md	bl	bl/md	md incis	md root	incis/md	root/md	buc ht	md/buc ht
P. africanus									
M 32363	7·0	6·1	87·2	6·6	5·3	94·3	75·7	8·9	78·7
RU 1769	7·8	5·8	74·4	6·6	5·5	84·6	70·5	8·6	90·7
1831	7·5	5·4	72·0	–	5·4	–	72·0	9·2	81·5
1933	7·5	5·7	76·0	5·9	5·7	78·7	76·0	7·5	100·0
1968	7·5	5·4	72·0	–	4·4	–	58·7	–	–
1979	7·3	5·7	72·4	5·5	5·0	75·4	68·5	10·1	72·3
2036	7·7	5·1	66·2	6·6	4·9	85·8	63·8	8·5	90·5
2040	6·8	5·5	80·8	–	5·0	–	73·5	–	–
Mean	7·4	5·6	75	6·2	5·2	84	69	8·8	87
Number	8	8	8	5	8	5	8	6	6
P. nyanzae									
RU 1677	9·2	7·0	76·1	8·4	6·1	91·3	66·3	10·4	88·5
1681	9·8	7·2	73·5	7·7	6·8	78·6	69·4	11·0	89·1
1685	8·3	6·9	83·1	5·5	6·4	66·3	77·2	11·9	69·7
1712	8·6	6·8	79·0	7·0	6·1	81·4	70·9	10·2	84·4
1713	9·0	6·7	74·5	–	6·5	–	72·2	11·5	78·3
1714	9·0	7·2	80·0	7·8	6·7	86·6	74·5	10·9	82·6
1803	9·5	–	–	7·2	–	75·8	–	10·6	89·6
1951	9·4	6·5	69·2	–	7·0	–	74·5	–	–
1975	9·4	6·4	68·1	7·4	7·3	78·7	77·6	10·6	88·7
1996	10·4	8·6	82·7	–	8·9	–	85·6	10·7	97·2
MB 104*	9·8	7·4	75·5	7·7	7·3	78·5	74·5	11·0	89·0
Mean	9·3	7·0	76	7·3	6·9	80	74	10·9	85
Number	10	9	9	7	9	7	9	9	9
P. major									
M 14297	11·0	8·3	75·5	9·0	7·8	81·8	71·0	12·6	87·3
UM-P 62-11	10·8	9·0	83·4	–	–	–	–	–	–
Mean	10·9	8·7	79	9·0	7·8	82	71	12·6	87
Number	2	2	2	1	1	1	1	1	1

* Not included in calculation of sample parameters.

Table 4 Measurements of upper I2.

	md	bl	bl/md	md/root	root/md	buc ht	md/buc ht
D. macinnesi							
RU 1825	4·0	4·9	122·5	3·7	92·5	6·5	61·5
1849	3·5	4·4	125·8	–	–	5·8	60·3
1850	3·4	4·3	126·4	–	–	6·2	54·8
1901	4·1	4·8	117·1	–	–	6·6	62·2
1906	3·0	4·6	153·2	–	–	–	–
1938	2·9	4·0	138·0	–	–	–	–
1969	4·3	4·4	102·3	3·2	74·4	7·0	61·4
MW 41	3·9	5·5	141·0	3·0	77·0	6·6	59·1

Table 4 (*cont.*)

	md	bl	bl/md	md/root	root/md	buc ht	md/buc ht
D. macinnesi (*cont.*)							
SO 417*	3·4	4·2	123·6	–	–	6·1	50·8
461*	3·9	4·4	112·9	3·2	82·1	6·4	61·0
1048*	4·0	4·4	110·0	2·8	–	5·8	–
Mean	3·6	4·6	128	3·3	81	6·5	60
Number	8	8	8	3	3	6	6
P. (R.) gordoni							
SO 550	5·8	6·0	103·4	4·8	82·7	7·4	78·4
Mean	5·8	6·0	103	4·8	83	7·4	78
Number	1	1	1	1	1	1	1
L. legetet							
SO 546	3·6	3·5	97·2	–	–	4·7	76·6
Mean	3·6	3·5	97	–	–	4·7	77
Number	1	1	1	–	–	1	1
P. africanus							
M 32363	5·0	6·0	120·0	–	–	7·0	71·4
RU 1769	5·6	5·9	105·3	3·7	66·0	7·1	78·9
1964	4·2	5·1	121·4	3·5	83·4	–	–
1998	5·5	6·2	112·8	4·0	72·7	7·3	75·3
2019	4·3	5·4	125·6	–	–	–	–
2036	5·1	5·1	100·0	3·4	66·7	6·6	77·3
MW 47	4·7	5·2	110·8	3·6	76·6	–	–
57	5·4	5·4	100·0	4·1	75·9	6·7	80·6
SO 549	4·5	4·8	106·7	3·8	84·5	5·2	86·5
Mean	4·9	5·5	111	3·7	75	6·7	78
Number	9	9	9	7	7	6	6
P. nyanzae							
RU 1674	5·5	6·2	112·8	–	–	7·5	73·3
1690	6·2	6·8	109·8	–	–	9·2	67·4
1704	6·6	6·9	104·5	–	–	9·0	73·4
2031	6·8	6·9	101·4	–	–	–	–
2035	5·8	6·1	105·2	–	–	8·0	72·5
2039	7·3	7·7	105·4	–	–	9·6	76·1
Mean	6·4	6·8	107	–	–	8·7	73
Number	6	6	6	–	–	5	5
P. major							
SO 554	7·3	7·5	102·7	–	–	9·5	76·8
UM-P 62-11	8·6	9·6	111·6	–	–	10·9	78·9
66-03	8·2	10·1	123·1	–	–	–	–
Mean	8·0	9·1	112	–	–	10·2	78
Number	3	3	3	–	–	2	2

* Not included in calculation of sample parameters.

Table 5 Measurements of upper C.

	max l	perp b	b/l	buc ht	max l / ht
D. macinnesi (Rusinga Island)					
M 32233	8·7	6·6	75·8	–	–
M 32230	8·9	6·3	70·7	–	–
RU 1649	6·1	4·7	77·0	7·6	80·3
1666	6·7	5·0	74·6	–	–
1682	9·6	6·6	68·6	–	–
1774	7·2	5·5	76·4	–	–
1775	8·5	6·1	71·8	–	–
1806	8·4	6·4	76·3	12·0	70·0
1843	8·3	5·6	67·5	–	–
1849	9·2	6·1	66·4	14·9	61·7
1850	7·0	5·4	77·2	–	–
1860	7·3	5·2	71·2	–	–
1875	6·5	4·9	75·4	–	–
1883	7·0	4·7	67·1	8·2	85·4
1895	8·8	6·2	70·5	–	–
1905	8·9	6·2	69·6	–	–
1948	8·6	6·2	72·1	15·8	54·4
1963	6·6	4·9	74·2	–	–
1966	9·9	6·4	64·6	16·1	61·5
1985	7·3	5·0	68·5	8·6	84·9
1988	9·3	5·7	61·3	–	–
2020	7·1	5·2	73·2	8·9	79·8
2041	8·2	6·1	74·4	9·3	88·2
2068	6·6	4·6	69·7	–	–
Mean	7·9	5·6	72	11·3	70
Number	24	24	24	9	9
S.D.	1·16	0·67	4·31	–	–
Coef. var.	14·7	8·2	8·6	–	–
S.E.	0·24	0·14	0·90	–	–
95% conf.	5·5	4·2	63	–	–
limits	10·3	6·0	81	–	–
D. macinnesi (Songhor)					
SO 402	8·3	6·5	78·3	–	–
414	7·5	5·6	74·6	10·1	74·3
417	8·4	6·6	78·6	–	–
519	7·6	5·7	75·0	–	–
520	7·8	5·8	74·4	11·0	70·9
539	6·9	5·7	82·6	–	–
580	7·7	5·7	74·0	–	–
581	8·0	5·7	71·2	–	–
582	8·8	6·1	69·3	14·8	59·4
952	7·2	5·5	76·4	–	–
1137	7·6	5·6	73·7	10·4	73·0
Mean	7·8	5·9	76	11·6	69
Number	11	11	11	4	4
S.D.	0·55	0·37	3·94	–	–
Coef. var.	7·1	6·3	5·2	–	–
S.E.	0·17	0·11	1·18	–	–
95% conf.	6·6	5·1	67	–	–
limits	9·0	6·7	85	–	–

Table 5 (*cont.*)

	max l	perp b	b/l	buc ht	max l / ht
P. (R.) gordoni					
SO 419	11·3	8·4	74·4	–	–
467	10·9	7·5	68·8	11·0	99·1
521	10·6	7·5	70·8	–	–
531	11·4	8·3	72·9	–	–
700	12·4	8·0	64·5	–	–
RU 1686	10·3	7·0	68·0	–	–
1788	11·4	8·2	72·0	–	–
Mean	11·0	7·8	72	11·0	99
Number	7	7	7	1	1
S.D.	0·80	0·50	4·95	–	–
Coef. var.	7·3	6·4	6·9	–	–
S.E.	0·28	0·18	1·75	–	–
95% conf.	9·1	6·3	60	–	–
limits	12·9	9·8	84	–	–
L. legetet					
RU 1995	6·0	4·8	80·0	8·6	69·8
SO 370	5·6	4·5	80·4	7·4	75·7
403	5·4	4·2	77·8	7·0	77·1
421	6·0	4·3	71·7	–	–
423	5·7	4·6	80·7	7·9	72·1
443	5·4	4·5	83·3	–	–
538	5·2	4·0	76·9	–	–
572	6·1	4·9	80·4	9·0	67·8
573	6·8	5·2	76·5	–	–
Mean	5·8	4·6	79	7·9	73
Number	9	9	9	5	5
S.D.	0·49	0·37	3·36	–	–
Coef. var.	8·4	8·1	4·3	–	–
S.E.	0·16	0·12	1·12	–	–
95% conf.	4·7	3·7	71	–	–
limits	6·9	5·5	8·7	–	–
P. africanus					
M 14084	11·4	8·2	72·0	15·2	75·0
M 32363	9·9	8·2	82·8	12·9	76·7
RU 1688	8·3	6·7	80·7	9·8	84·7
1705	9·0	7·3	81·1	–	–
1707	8·9	7·0	78·7	10·6	84·0
1723	10·7	7·7	72·0	–	–
1769	9·4	7·1	75·5	–	–
1797	10·8	7·4	68·5	–	–
1830	9·5	7·5	78·9	–	–
1871	9·2	7·7	83·7	–	–
1897	11·2	8·4	75·0	–	–
1900	8·2	6·8	83·0	–	–
1912	9·3	7·0	75·3	–	–
1913	9·1	6·7	73·6	–	–
1942	9·7	7·1	73·2	–	–
1974	7·7	6·9	89·6	10·4	74·1

Table 5 (*cont.*)

	max l	perp b	b/l	buc ht	max l / ht
P. africanus (*cont.*)					
2049	9·4	7·0	74·5	11·6	81·0
2088	12·6	8·7	69·1	–	–
MW 46	9·1	6·9	75·8	–	–
Mean	9·7	7·4	77	11·8	81
Number	19	19	19	6	6
S.D.	0·61	5·47	–	–	–
Coef. var.	12·5	8·2	7·1	–	–
S.E.	0·28	0·14	1·25	–	–
95% conf.	7·2	6·1	65	–	–
limits	12·2	8·7	89	–	–
P. nyanzae					
M 16647	15·1	11·6	76·8	21·0	71·9
RU 1677	13·8	10·9	79·0	19·0	72·6
1684	14·4	11·2	77·8	17·2	83·7
1687	11·7	9·8	83·8	–	–
1763	13·5	11·1	82·2	–	–
1812	12·2	9·0	73·8	–	–
1813	14·2	11·5	80·9	–	–
1815	12·1	10·1	83·5	–	–
1845	12·7	10·0	78·6	–	–
1971	12·3	10·2	82·9	–	–
Mean	13·2	10·5	80	19·1	76
Number	10	10	10	3	3
S.D.	1·16	0·85	3·29	–	–
Coef. var.	8·8	8·1	4·1	–	–
S.E.	0·37	0·27	1·04	–	–
95% conf.	10·6	8·6	73	–	–
limits	15·8	12·4	87	–	–
P. major					
SO 584	16·2	13·3	82·1	–	–
585	19·5	14·7	75·4	–	–
LS 8	17·2	12·2	70·9	–	–
UM-P 62-03	18·7	15·7	84·0	25·0	70·8
62-04	19·3	16·0	83·0	22·0	87·7
62-05	18·8	16·1	85·6	22·5	83·5
62-11	18·6	15·7	84·4	27·6	67·3
62-12	17·6	16·1	91·5	22·0	80·0
Mean	18·2	15·0	82	23·8	79
Number	8	8	8	5	5
S.D.	1·14	1·47	6·33	–	–
Coef. var.	6·3	9·8	7·7	–	–
S.E.	0·40	0·52	2·24	–	–
95% conf.	15·5	11·5	67	–	–
limits	20·9	18·5	97	–	–

Table 6 Measurements of upper P3.

	md buc	md ling	bl	bl/md	md ling/md buc	height buc	height ling	buc ht/ling ht	(md+bl)/2	P³/M¹
D. macinnesi										
M 32231	4·3	3·9	6·5	158·5	90·7	6·5	4·0	162·5	5·3	–
M 32337*	4·1	3·6	7·0	184·1	87·8	6·0	3·0	200·0	5·4	–
RU 1774	4·5	3·6	6·9	170·4	80·0	7·1	4·2	169·0	5·5	80·9
1849	4·5	4·0	7·0	164·8	88·9	6·9	4·5	153·3	5·6	81·2
1850	4·1	3·5	6·8	179·0	85·4	6·8	3·5	194·3	5·3	79·1
SO 417*	4·5	4·0	5·8	136·5	88·9	5·5	2·6	210·5	5·0	–
Mean	4·3	3·8	6·8	168	87	6·8	4·1	170	5·5	80
Number	4	4	4	4	4	4	4	4	4	3
P. (R.) gordoni										
RU 1894	5·6	4·9	7·4	142·4	87·5	6·3	5·2	121·1	6·4	–
SO 700	5·8	5·5	8·3	146·9	94·8	7·0	4·8	145·9	7·0	84·4
Mean	5·7	5·2	7·9	145	91	6·7	5·0	134	6·7	84
Number	2	2	2	2	2	2	2	2	2	1
P. (R.) vancouveringi										
RU 1778	5·3	5·3	6·8	128·3	100·0	5·2	4·8	108·2	6·1	88·4
MB 53	5·3	5·3	6·7	126·4	100·0	6·0	5·6	107·1	6·0	–
Mean	5·3	5·3	6·8	127	100	5·6	5·2	108	6·1	88
Number	2	2	2	2	2	2	2	2	2	2
L. legetet										
SO 421	4·2	3·4	5·9	155·3	80·9	3·7	3·3	112·1	4·9	–
443	3·3	3·0	5·3	168·0	90·9	4·2	2·7	155·6	4·2	73·7
538	4·0	3·0	5·1	145·6	75·0	–	–	–	4·3	–
1086	3·6	3·0	4·6	139·2	83·4	3·8	2·5	152·0	4·1	–
Mean	3·8	3·1	5·2	148	83	3·9	2·8	141	4·4	74
Number	4	4	4	4	4	3	3	3	4	1
P. africanus										
M 14084	7·4	5·1	9·4	149·2	68·9	8·4	5·1	164·8	7·8	89·0
M 32363	6·2	5·1	9·8	172·0	82·2	8·5	5·1	166·8	7·7	89·0
RU 1705	5·6	4·2	8·7	177·7	75·0	6·2	4·3	144·1	6·8	85·0
SO 596	5·6	4·5	7·8	154·4	80·4	6·1	3·5	174·3	6·4	–
Mean	6·2	4·7	8·9	163	77	7·3	4·5	163	7·2	88
Number	4	4	4	4	4	4	4	4	4	4
P. nyanzae										
M 16647	7·7	6·5	11·3	159·1	84·4	10·9	6·3	173·0	9·2	87·6
16649	8·5	6·6	12·5	164·2	77·6	8·7	6·1	142·7	10·0	91·8
RU 1674	6·8	5·3	10·5	173·6	77·9	7·2	4·5	160·0	8·3	87·2
1677	7·8	6·3	10·9	154·6	80·8	11·1	6·7	165·6	9·0	87·4
1718	6·8	5·7	10·3	164·9	83·9	7·9	5·7	138·5	8·3	–
1874	7·2	6·3	11·1	164·4	87·5	8·9	5·6	160·0	8·9	–
Mean	7·5	6·1	11·1	163	82	9·1	5·8	157	9·0	89
Number	6	6	6	6	6	6	6	6	6	4

*Not included in calculation of sample parameters.

Table 6 (*cont.*)

	md buc	md ling	bl	bl/md	md ling / md buc	height buc	height ling	buc ht / ling ht	(md+bl)/2	P³/M¹
P. major										
M 14331*	9·1	8·2	13·1	150·5	90·2	10·7	6·9	155·0	10·9	–
SO 418	8·6	5·4	10·6	151·4	62·8	–	–	–	8·3	80·5
527	8·0	5·6	10·0	147·0	70·0	–	–	–	8·4	–
529	8·2	7·0	11·7	153·9	85·4	9·8	6·1	160·6	9·7	–
UM-P 62-11	10·6	8·1	14·6	155·2	76·4	–	–	–	12·0	99·2
Mean	8·9	6·5	11·7	149	74	9·8	6·1	161	9·6	90
Number	4	4	4	4	4	1	1	1	4	2

* Not included in calculation of sample parameters.

Table 7 Measurements of upper P4.

	md	bl	bl/md	height buc	height ling	buc ht / ling ht	(md+bl)/2	P⁴/M¹
D. macinnesi								
RU 1774	4·2	6·7	159·7	5·2	3·4	152·9	5·5	80·9
1806	4·3	6·8	158·1	3·9	2·8	139·2	5·6	81·2
1849	4·3	7·3	169·8	5·1	4·7	108·4	5·8	84·1
1850	3·8	6·8	179·0	4·3	3·8	113·2	5·3	79·1
2076	4·4	7·2	163·7	–	–	–	5·8	–
2086	3·8	7·5	197·5	–	–	–	5·7	76·0
SO 417*	4·3	6·1	141·9	4·7	3·6	130·6	5·2	–
Mean	4·1	7·1	172	4·6	3·6	129	5·5	81
Number	6	6	6	4	4	4	6	5
P. (R.) gordoni								
SO 401	5·6	7·2	128·7	–	–	–	6·4	80·0
488	5·6	7·9	141·1	–	–	–	6·8	–
700	6·0	8·0	133·3	5·4	4·7	114·8	7·0	84·2
1081	5·3	7·2	135·9	5·1	4·4	115·9	6·3	–
Mean	5·6	7·6	135	5·3	4·6	115	6·7	82
Number	4	4	4	2	2	2	4	2
P. (R.) vancouveringi								
RU 1778	5·6	6·7	119·6	5·2	5·2	100·0	6·2	89·8
2058	4·9	6·2	126·5	–	–	–	5·6	83·6
Mean	5·3	6·5	123	5·2	5·2	100	5·9	86
Number	2	2	2	1	1	1	2	2
L. legetet								
SO 443	3·4	5·3	155·8	3·7	3·0	123·0	4·4	77·2

* Not included in calculation of sample parameters.

Table 7 (*cont.*)

	md	bl	bl/md	height buc	height ling	buc ht/ling ht	(md+bl)/2	P^4/M^1
P. africanus								
M 14084	5·7	9·0	158·0	7·4	5·7	129·7	7·4	84·0
32363	5·2	9·8	188·4	–	–	–	7·5	85·0
RU 1705	4·9	8·5	173·6	5·1	4·1	124·3	6·7	84·0
1733	5·8	9·9	170·9	7·7	5·8	132·8	7·9	–
2036	4·9	8·5	173·6	5·8	4·9	118·3	6·7	76·0
2088	5·5	9·4	171·0	–	–	–	7·5	82·0
MW 43	5·8	9·5	163·9	7·5	5·9	127·0	7·7	–
82	5·5	8·5	154·5	–	–	–	7·0	–
SO 524	5·6	9·6	171·5	6·4	6·0	106·8	7·6	–
Mean	5·4	9·2	170	6·7	5·4	123	7·3	82
Number	9	9	9	6	6	6	9	5
P. nyanzae								
M 16647	6·7	11·7	174·6	8·4	5·9	142·3	9·2	87·6
16649	7·7	12·0	155·8	6·9	6·3	109·3	9·9	91·6
RU 1674	6·1	11·2	183·6	6·0	4·2	142·8	8·6	91·4
1677	7·0	10·8	154·2	8·4	7·0	120·0	8·9	86·4
1691	6·8	9·6	141·1	7·0	4·9	143·0	8·2	–
1715	7·3	10·8	140·8	7·2	6·6	109·1	9·1	–
1718	6·4	10·6	165·8	7·4	6·5	113·9	8·5	–
1719	6·4	10·4	162·5	7·4	6·6	112·1	8·4	–
1732	7·7	11·5	149·3	7·2	6·8	106·0	9·6	–
2005	6·0	11·0	183·3	–	–	–	8·5	–
2037	6·2	10·9	175·9	–	–	–	8·6	–
Mean	6·8	11·0	163	7·3	6·1	122	8·9	89
Number	11	11	11	9	9	9	11	4
S.D.	0·61	0·66	14·72	–	–	–	–	–
Coef. var.	9·0	6·0	9·0	–	–	–	–	–
S.E.	0·18	0·20	4·44	–	–	–	–	–
95% conf.	5·3	9·5	130	–	–	–	–	–
limits	8·1	12·5	196	–	–	–	–	–
P. major								
SO 418	6·1	11·2	183·5	6·0	4·2	143·0	8·7	84·5
441	7·4	11·5	155·3	5·5	4·0	137·3	9·5	–
527	6·4	10·2	159·3	–	–	–	8·3	–
529	7·6	11·6	152·9	7·8	5·5	141·9	9·6	–
UM-P 62-11	7·9	14·7	186·0	–	–	–	11·3	93·3
69-01	7·5	13·6	181·2	–	–	–	10·6	–
Mean	7·2	12·1	170	6·4	4·6	141	9·7	95
Number	6	6	6	3	3	3	6	2

Table 8 Measurements of upper M1.

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$
D. macinnesi				
RU 1669	5·4	7·1	131·6	6·3
1774	6·0	7·5	125·0	6·8
1788	6·0	7·0	116·7	6·5
1796	5·7	7·7	135·1	6·7
1799	5·5	6·9	125·4	6·2
1806	6·0	7·8	130·0	6·9
1849	6·2	7·5	121·0	6·9
1850	5·8	7·5	129·3	6·7
1901	6·2	8·1	130·6	7·1
1946	5·6	7·7	137·7	6·7
1991	6·2	7·4	119·3	6·8
2028	6·0	7·5	125·0	6·8
2086	6·5	8·4	129·2	7·5
M 14082	5·7	6·6	115·8	6·2
Mean	5·9	7·5	127	6·8
Number	14	14	14	14
S.D.	0·31	0·47	6·61	0·34
Coef. var.	5·3	6·3	5·2	5·0
S.E.	0·08	0·12	1·77	0·09
95% conf.	5·2	6·5	113	6·1
limits	6·6	8·5	141	7·5
P. (R.) gordoni				
MW 52	8·4	8·0	95·3	8·2
SO 401	8·1	7·9	97·5	8·0
487	8·4	7·9	94·1	8·2
700	8·5	8·1	95·3	8·3
930	8·1	8·5	104·9	8·3
931	8·1	8·0	98·8	8·1
932	7·8	8·0	102·6	7·9
Mean	8·2	8·1	98	8·1
Number	7	7	7	7
S.D.	0·24	0·21	4·05	0·15
Coef. var.	2·9	2·6	4·1	1·9
S.E.	0·09	0·08	1·53	0·06
95% conf.	7·6	7·6	88	7·7
limits	8·8	8·6	108	8·5
P. (R.) vancouveringi				
RU 1778	7·0	6·8	97·2	6·9
1801	6·4	6·6	103·0	6·5
2058	6·8	6·5	95·6	6·7
SO 944	6·8	6·4	94·2	6·6
1134	6·5	6·5	100·0	6·5
MB 125	7·1	6·7	94·4	6·9
Mean	6·8	6·6	97	6·7
Number	6	6	6	6
S.D.	0·27	0·15	2·48	0·18
Coef. var.	4·0	2·2	2·6	2·7
S.E.	0·11	0·06	1·42	0·07
95% conf.	6·1	6·2	91	6·3
limits	7·5	7·0	103	7·1

Table 8 (*cont.*)

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$
L. legetet				
SO 413	4·9	6·6	134·7	5·8
443	5·1	6·2	121·6	5·7
536	5·3	6·5	122·8	5·9
537	4·8	5·9	123·0	5·4
926	5·1	6·2	121·6	5·7
Mean	5·0	6·3	125	5·7
Number	5	5	5	5
S.D.	0·19	0·28	4·02	0·19
Coef. var.	3·8	4·5	3·3	3·3
S.E.	0·09	0·12	1·8	0·08
95% conf.	4·5	5·5	110	5·2
limits	5·5	7·1	132	6·2
P. africanus				
M 14081	7·0	8·4	120·0	7·7
14084	7·9	9·6	121·5	8·8
14085	7·8	8·9	114·1	8·4
32363	7·8	9·5	121·9	8·7
RU 1705	7·4	8·6	116·2	8·0
1741	8·4	9·8	116·7	9·1
1742	8·5	9·8	115·3	9·2
1795	8·0	9·0	112·5	8·5
1904	7·4	8·7	117·6	8·1
1934	7·6	9·9	130·2	8·8
1936	7·7	9·1	118·2	8·4
1973	7·1	8·0	112·8	7·6
2036	7·8	9·8	125·6	8·8
2088	8·6	9·6	111·6	9·1
MW 61	8·2	9·8	119·4	9·0
SO 528	7·0	8·5	121·3	7·8
Mean	7·8	9·2	118	8·5
Number	15	15	15	15
S.D.	0·48	0·61	5·11	0·51
Coef. var.	6·2	6·6	2·8	6·0
S.E.	0·12	0·16	1·32	0·13
95% conf.	6·8	7·9	108	7·4
limits	8·8	10·5	128	9·6

Table 8 (*cont.*)

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$
P. nyanzae				
M 16647	9·2	11·7	127·2	10·5
16649	10·2	11·6	113·7	10·9
RU 1674	8·4	10·3	123·8	9·4
1677	9·4	11·2	119·1	10·3
1696	11·0	12·2	110·9	11·6
1720	9·7	11·5	118·6	10·6
1721	10·7	12·4	115·9	11·6
1803	9·2	9·8	106·5	9·5
1929	10·3	11·3	109·6	10·8
MB 107	10·6	11·3	106·6	11·0
Mean	9·9	11·3	115	10·7
Number	10	10	10	10
S.D.	0·86	0·79	7·36	0·77
Coef. var.	8·7	7·0	6·4	7·2
S.E.	0·27	0·25	2·33	0·24
95% conf.	7·9	9·5	98	9·0
limits	11·8	13·1	132	12·4
P. major				
SO 418	9·3	11·3	121·5	10·3
542	10·5	12·8	121·9	11·7
933	11·4	12·2	107·0	11·8
934	10·1	11·6	114·9	10·9
939	9·7	10·9	112·4	10·3
UM-P 62-07	11·4	13·9	122·0	12·7
62-11	11·7	12·7	108·5	12·1
64-01	12·0	13·9	115·8	13·0
66-41	12·0	14·0	116·6	13·0
69-02	11·0	13·3	121·0	12·2
Mean	10·9	12·7	116	11·8
Number	10	10	10	10
S.D.	0·96	1·13	5·55	1·01
Coef. var.	8·8	8·9	4·8	8·6
S.E.	0·30	0·36	1·76	0·32
95% conf.	8·2	10·2	103	9·5
limits	13·1	15·2	129	11·7

Table 9 Measurements of upper M2.

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$	$\frac{M^2}{M^1}$
D. macinnesi					
RU 1669	5·8	7·1	122·4	6·5	103·2
1774	6·7	8·0	119·4	7·4	108·8
1776	6·6	7·8	118·1	7·2	–
1799	5·8	6·9	119·0	6·4	103·2
1806	7·4	8·8	119·0	8·1	117·4
1849	7·1	8·1	114·2	7·6	110·2
1850	6·7	8·0	119·4	7·4	110·4
1862	7·0	8·9	127·2	8·0	–
1866	6·4	8·2	128·1	7·3	–
1901	7·2	8·5	118·1	7·8	109·8
1915	6·6	8·0	121·2	7·3	–
2028	6·4	7·8	121·9	7·1	–
2086	7·2	8·7	120·9	8·0	107·0
Mean	6·7	8·1	121	7·4	109
Number	13	13	13	13	8
S.D.	0·50	0·60	3·73	0·53	–
Coef. var.	7·5	7·4	3·1	7·2	–
S.E.	0·14	0·17	1·03	0·15	–
95% conf.	5·6	6·8	113	6·2	–
limits	7·8	9·4	129	8·6	–
P. (R.) gordoni					
MW 52	9·2	8·6	93·5	8·9	108·4
SO 375	10·0	10·4	104·0	10·2	–
449	9·6	10·4	108·3	10·0	–
700	9·6	10·0	104·2	9·8	118·0
938	9·5	10·0	105·3	9·8	–
Mean	9·6	9·9	103	9·7	113
Number	5	5	5	5	2
P. (R.) vancouveringi					
RU 2058	7·8	7·4	94·8	7·6	113·3
L. legetet					
SO 436	5·4	7·1	131·4	6·3	–
535	5·8	7·0	120·8	6·4	–
537	5·1	6·3	123·6	5·7	105·5
927	5·4	6·8	126·0	6·1	–
929	5·4	6·8	126·0	6·1	–
935	5·8	7·0	120·8	6·4	–
936	5·4	6·9	127·9	6·2	–
MB 109	5·6	6·8	121·3	6·2	–
Mean	5·5	6·8	125	6·2	106
Number	8	8	8	8	1
S.D.	0·24	0·24	3·81	0·23	–
Coef. var.	4·4	3·5	3·6	3·7	–
S.E.	0·08	0·09	1·35	0·08	–
95% conf.	4·9	6·2	116	5·7	–
limits	6·1	7·4	134	6·7	–

Table 9 (*cont.*)

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$	$\frac{M^2}{M^1}$
P. africanus					
M 14081	7·5	9·4	125·3	8·5	110·0
14084	9·2	11·3	122·8	10·3	117·0
32363	9·2	10·8	117·4	10·0	115·0
RU 1671	7·8	9·7	124·3	8·8	–
1672	8·1	9·5	117·3	8·8	–
1747	8·9	10·9	122·4	9·9	–
1835	8·9	10·8	121·2	9·9	–
1861	8·9	10·2	114·7	9·6	–
1872	9·3	11·0	118·3	10·2	–
1873	8·4	10·5	125·0	9·5	–
1904	7·7	9·4	122·0	8·6	106·0
1954	7·9	9·3	117·8	8·6	–
1973	7·9	9·3	117·8	8·6	–
1981	7·8	9·6	123·0	8·7	–
2016	8·7	10·1	116·1	9·4	–
2026	9·8	12·0	122·4	10·9	–
2036	8·1	9·9	122·2	9·0	102·0
2088	9·8	11·0	112·3	10·4	114·0
SO 946	9·2	11·6	126·2	10·6	–
1078	8·1	10·2	126·0	9·2	–
Mean	8·5	10·3	120	9·5	111
Number	20	20	20	20	6
S.D.	0·72	0·82	3·99	0·76	–
Coef. var.	8·5	8·0	3·3	8·0	–
S.E.	0·16	0·18	0·89	0·17	–
95% conf.	7·0	8·6	112	7·9	–
limits	10·0	12·0	129	11·1	–
P. nyanzae					
M 16647	12·2	13·4	109·8	12·8	122·0
RU 1674	9·9	11·5	116·1	10·7	114·0
1677	12·0	13·5	112·5	12·8	124·0
1803	10·5	11·8	112·3	11·2	118·0
KA 6	11·1	12·5	112·6	11·8	–
Mean	11·3	12·5	113	11·9	120
Number	5	5	5	5	4
P. major					
SO 381	12·1	14·2	117·3	13·2	–
382	12·8	16·0	125·0	14·4	–
485	14·7	16·8	114·3	15·8	–
LS 7	10·8	14·6	135·1	12·7	–
UM-P 62-08	15·1	17·0	112·5	16·2	–
62-11	13·1	14·0	106·9	13·6	112·0
Mean	12·7	14·9	119	13·8	112
Number	6	6	6	6	1

Table 10 Measurements of upper M3.

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$	$\frac{M^3}{M^1}$
D. macinnesi					
RU 1670	7·0	8·0	114·3	7·5	–
1774	6·2	7·9	127·3	7·1	104·4
1799	5·2	6·6	126·9	5·9	95·2
1806	6·7	7·9	117·9	7·3	105·8
1849	6·4	7·9	123·3	7·2	104·3
1850	6·6	7·8	118·1	7·3	109·0
1901	6·9	8·5	123·2	7·7	108·4
1915	5·8	7·6	131·0	6·7	–
2054	7·0	8·2	117·1	7·6	–
SO 457*	6·3	8·0	127·0	7·2	–
Mean	6·4	7·8	122	7·1	105
Number	9	9	9	9	6
S.D.	0·62	0·52	6·01	0·55	–
Coef. var.	9·7	6·7	4·9	7·8	–
S.E.	0·21	0·17	2·00	0·18	–
95% conf.	5·0	6·6	108	5·8	–
limits	7·8	8·9	136	8·4	–
P. (R.) gordoni					
RU 1692	12·2	11·7	96·0	12·0	–
SO 700	10·3	10·7	103·9	10·5	127
943	9·9	9·7	98·0	9·8	–
Mean	10·8	10·7	99	10·8	127
Number	3	3	3	3	1
P. (R.) vancouveringi					
RU 2058	8·3	7·5	90·4	7·9	117·9
MW 48	7·2	7·4	102·8	7·3	–
SO 942	7·8	8·1	103·8	8·0	–
Mean	7·8	7·7	99	7·7	118
Number	3	3	3	3	1
L. legetet					
SO 412	4·8	5·7	118·7	5·3	–
459	5·6	7·0	125·1	6·3	–
462	5·7	7·1	124·6	6·4	–
535	5·5	6·3	114·4	5·9	–
940	5·5	7·2	130·9	6·4	–
941	5·4	6·8	126·0	6·1	–
Mean	5·4	6·7	123	6·0	–
Number	6	6	6	6	–
S.D.	0·32	0·58	6·71	0·50	–
Coef. var.	5·9	8·6	5·4	8·3	–
S.E.	0·13	0·24	2·74	0·21	–
95% conf.	4·6	5·2	108	4·7	–
limits	6·2	8·2	140	7·3	–

Table 10 (*cont.*)

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$	$\frac{M^3}{M^1}$
P. africanus					
M 14084	7·9	10·5	132·9	9·2	105·0
32363	8·4	11·0	130·9	9·7	111·0
RU 1821	7·6	9·9	130·2	8·8	–
1920	7·9	10·5	132·9	9·2	–
1922	8·8	10·9	123·9	9·9	–
2088	9·3	11·5	123·8	10·4	114·0
SO 442	8·5	11·4	134·1	10·0	–
Mean	8·3	10·8	130	9·6	110
Number	7	7	7	7	3
S.D.	0·59	0·56	4·08	0·56	–
Coef. var.	7·1	5·2	3·1	5·8	–
S.E.	0·22	0·21	1·54	0·21	–
95% conf.	6·8	9·4	120	8·2	–
limits	9·8	12·2	140	11·0	–
P. nyanzae					
M 16647	11·1	14·1	127·0	12·6	120·0
RU 1674	10·1	12·6	124·8	11·4	121·0
1677	11·8	13·9	117·8	12·9	125·0
1697	12·4	14·8	119·3	13·6	–
1836	12·0	13·1	109·1	12·5	–
1910	10·1	12·5	123·8	11·3	–
2061	11·7	14·0	119·6	12·9	–
Mean	11·3	13·6	120	12·5	122
Number	7	7	7	7	3
S.D.	0·92	0·86	5·92	0·83	–
Coef. var.	8·1	6·3	4·9	6·6	–
S.E.	0·35	0·32	2·24	0·32	–
95% conf.	9·0	11·5	105	10·5	–
limits	13·6	15·7	135	14·5	–
P. major					
M 14331	14·6	17·8	121·9	16·2	–
LS 7	10·4	13·6	130·8	12·0	–
UM-P 62-11	12·7	14·3	112·6	13·5	112·0
Mean	12·6	15·2	121	13·9	112
Number	3	3	3	3	1

* Not included in calculation of sample parameters.

Table 11 Measurements of lower I1.

	md	bl	bl/md	md/incis	md/root	incis/md	root/md	buc ht	md/buc ht
D. macinnesi									
RU 900	2·7	3·7	137·0	2·7	1·9	100·0	70·4	5·1	52·9
SO 395*	3·3	4·0	121·3	3·3	2·5	100·0	75·7	6·6	50·0
Mean	2·7	3·7	137	2·7	1·9	100	70	5·1	53
Number	1	1	1	1	1	1	1	1	1
P. (R.) gordoni									
SO 428	4·3	4·7	109·3	4·0	3·1	93·0	72·1	10·1	42·6
473	3·9	4·4	112·8	3·9	3·0	100·0	76·9	7·7	50·7
475	5·6	4·8	85·7	5·2	4·6	92·9	80·7	10·3	54·4
555	5·9	4·9	83·1	5·6	4·8	94·9	81·4	8·4	70·2
556	4·7	4·8	102·1	4·7	3·5	100·0	74·5	10·7	43·9
563	4·3	4·8	111·7	4·3	3·5	100·0	81·4	10·1	42·6
Mean	4·8	4·8	101	4·6	3·8	97	77	9·6	51
Number	6	6	6	6	6	6	6	6	6
L. legetet									
SO 545	2·3	3·4	147·8	–	1·7	–	73·9	–	–
1076	2·8	3·0	107·1	–	–	–	–	–	–
KO 8	2·9	3·0	103·5	2·6	2·0	89·6	69·7	4·8	60·4
Mean	2·7	3·1	119	2·6	1·9	90	71	4·8	60
Number	3	3	3	1	2	1	2	1	1
P. africanus									
M 32362*	3·5	4·6	131·3	–	–	–	–	–	–
32363	3·7	4·9	132·4	3·7	3·2	100·0	86·5	9·9	37·3
RU 1769	4·1	5·2	126·9	3·8	3·0	92·7	73·2	8·4	48·8
2036	4·0	5·0	125·0	–	–	–	–	–	–
2090	4·6	5·5	119·5	–	–	–	–	–	–
Mean	4·1	5·2	126	3·8	3·1	96	80	9·2	43
Number	4	4	4	2	2	2	2	2	2
P. nyanzae									
RU 1947	4·6	6·2	134·8	4·6	4·1	100·0	89·1	9·5	48·4
2030	6·0	5·8	96·7	5·5	4·6	91·7	76·7	9·7	62·8
MW 40	5·5	6·1	110·9	–	–	–	–	–	–
42	5·3	6·5	122·6	–	–	–	–	–	–
KA 5	5·0	5·8	116·0	–	–	–	–	–	–
Mean	5·3	6·1	115	5·1	4·4	96	83	9·6	55
Number	5	5	5	2	2	2	2	2	2
P. major									
UM-P 62-06	6·4	8·0	125·0	6·2	4·8	96·9	75·0	14·0	45·7

* Not included in calculation of sample parameters.

Table 12. Measurements of lower 12.

	md	bl	bl/md	md/root	root/md	buc ht	md/buc ht
D. macinnesi							
RU 900	2·9	4·3	148·3	2·0	68·9	5·6	51·8
1952	3·0	4·7	157·0	–	–	6·0	50·0
1953	3·4	4·3	126·4	–	–	–	–
1993	3·0	4·0	133·3	2·5	83·4	4·7	63·8
2017	3·7	4·3	116·2	3·0	81·1	5·9	62·7
2064	3·7	4·0	108·1	2·4	64·9	6·0	61·7
SO 517*	3·2	4·7	147·8	2·6	81·3	6·0	53·3
544*	3·5	4·7	134·3	3·0	85·7	6·0	58·3
Mean	3·3	4·3	132	2·7	75	5·6	59
Number	6	6	6	4	4	5	5
P. (R.) gordoni							
SO 383	4·5	5·3	117·8	3·8	84·5	11·3	39·8
557	4·2	4·5	107·2	3·3	78·6	7·2	58·3
558	4·7	5·5	117·0	3·6	76·6	–	–
559	4·6	5·0	106·3	3·6	78·3	7·5	61·3
560	4·8	5·6	116·7	3·8	79·2	7·0	68·6
562	4·5	5·3	117·8	3·8	81·4	11·3	39·8
Mean	4·6	5·2	113	3·6	79	8·9	52
Number	6	6	6	6	6	5	5
L. legetet							
SO 384	3·4	3·8	111·8	2·9	91·2	5·6	60·7
411	3·4	4·2	123·6	–	–	5·2	65·4
547	3·5	4·0	114·2	2·6	74·3	4·7	74·5
KO 8	2·9	3·2	110·2	2·6	89·7	5·2	55·7
Mean	3·3	3·8	115	2·7	85	5·2	64
Number	4	4	4	3	3	4	4
P. africanus							
M 32363	4·2	6·0	142·9	3·1	73·8	11·8	35·6
RU 1769	4·4	6·0	136·3	3·0	68·2	11·5	38·3
2036	4·6	5·5	119·6	2·7	58·7	9·4	48·9
SO 561	4·2	6·2	147·7	2·6	61·9	8·3	50·6
Mean	4·4	5·9	137	2·9	66	10·2	43
Number	4	4	4	4	4	4	4
P. nyanzae							
RU 1716	5·0	6·4	128·0	4·0	80·0	12·2	41·0
1730	4·7	6·8	144·8	3·8	80·8	9·9	47·4
1947	5·2	7·8	150·0	4·1	78·8	11·1	46·8
1982	5·6	8·0	142·8	4·4	78·8	–	–
Mean	5·1	7·2	143	4·1	80	11·1	46
Number	4	4	4	4	4	3	3
P. major							
SO 454	7·0	8·4	120·0	–	–	11·0	64·0
1135	4·7	7·0	149·0	4·2	89·4	11·5	40·8
Mean	5·9	7·7	135	4·2	89	11·3	52
Number	2	2	2	1	1	2	2

* Not included in calculation of sample parameters.

Table 13 Measurements of lower C.

	max l	perp b	b/l	buc ht	mesial ht	mesial ridge	ridge / ht	max l / buc ht
D. macinnesi								
M 32232	8·2	5·5	67·0	–	–	–	–	–
32338	7·0	4·6	65·7	8·5	6·8	4·1	60·3	82·4
RU 900	7·5	5·0	66·7	12·0	8·2	7·3	89·0	62·5
1650	6·2	4·1	66·1	8·4	5·0	3·0	60·0	73·8
1699	8·3	5·9	71·1	11·8	7·5	5·1	68·0	70·4
1700	8·2	5·4	65·8	12·0	9·0	7·2	80·0	68·4
1701	8·5	6·0	70·6	14·6	11·8	9·0	76·2	58·2
1702	6·6	3·9	59·1	9·3	7·4	5·1	68·9	71·0
1781	6·5	4·2	64·7	8·3	6·0	3·6	60·0	78·3
1811	9·2	5·8	63·0	11·0	7·2	4·2	58·3	83·6
1850	6·5	4·1	63·1	8·7	6·2	4·0	64·5	74·7
1857	9·2	6·0	65·2	–	–	–	–	–
1880	8·0	5·3	66·2	–	–	–	–	–
1902	7·8	5·6	71·8	12·0	9·8	6·8	69·1	65·0
1962	8·5	5·3	62·4	–	–	–	–	–
1972	8·5	5·4	63·5	13·5	7·7	5·1	66·2	63·0
1990	6·7	4·6	68·6	7·6	5·2	3·2	61·6	88·2
2007	7·6	4·8	63·2	–	–	–	–	–
2012	6·8	4·0	58·9	–	–	–	–	–
2013	8·0	5·5	68·7	–	–	–	–	–
2023	6·9	4·0	58·0	8·3	5·4	3·5	64·6	83·2
2024	6·4	4·0	62·5	8·5	6·5	4·2	64·6	75·3
2062	8·3	5·6	67·5	–	–	–	–	–
2063	6·5	4·1	63·1	8·9	6·1	4·9	80·3	73·1
SO 405*	7·5	5·0	66·7	9·1	–	–	–	82·5
429*	7·3	5·0	68·5	10·1	6·8	3·9	57·4	72·2
518*	7·6	5·0	65·8	9·7	6·5	3·8	58·5	78·4
574*	7·1	5·8	81·7	10·2	8·9	7·3	82·1	69·6
576*	8·2	5·3	64·6	10·1	7·0	3·5	50·0	81·2
1047*	7·5	5·1	68·0	10·1	6·8	4·3	63·3	74·5
1099*	7·7	5·6	72·7	8·1	5·9	3·7	62·7	95·0
Mean	7·6	5·0	65	10·3	7·3	5·1	69	73
Number	24	24	24	16	16	16	16	16
S.D.	0·94	0·76	3·70	2·20	1·86	1·75	8·86	8·48
Coef. var.	12·4	15·2	5·7	21·3	25·5	34·2	12·8	11·6
S.E.	0·20	0·16	0·77	0·57	0·48	0·45	2·29	2·19
95% conf.	5·6	3·4	57	5·6	3·3	1·3	50	55
limits	9·6	6·6	73	15·0	11·3	8·9	88	91
P. (R.) gordoni								
SO 373	11·3	8·5	75·2	15·7	12·7	10·4	81·9	72·0
1112	11·3	7·4	65·5	–	–	–	–	–
Mean	11·3	8·0	70	15·7	12·7	10·4	82	72
Number	2	2	2	1	1	1	1	1

* Not included in calculation of sample parameters.

Table 13 (*cont.*)

	max l	perp b	b/l	buc ht	mesial ht	mesial ridge	ridge/ht	max l/buc ht
L. legetet								
RU 1749	5·9	3·7	62·7	–	–	–	–	–
SO 386	6·7	4·6	68·7	–	–	–	–	–
398	6·1	4·3	70·5	9·4	7·2	5·0	69·4	64·9
452	6·2	4·4	71·0	–	–	–	–	–
516	6·4	4·4	68·7	9·5	7·2	4·6	63·9	67·4
567	6·0	4·3	71·6	7·8	6·0	4·0	66·7	76·9
568	5·1	3·7	72·6	6·4	5·2	2·9	55·7	79·7
569	6·0	4·4	73·4	7·4	5·6	2·4	42·8	81·1
570	7·0	4·5	64·3	9·6	6·6	3·5	53·1	72·9
571	6·0	4·3	71·7	9·1	6·7	5·1	76·1	65·9
1050	5·5	3·7	67·2	7·5	5·6	2·8	50·0	73·4
1075	6·0	4·4	73·4	9·5	7·0	4·5	64·2	63·2
1102	5·8	3·7	63·7	8·2	6·0	3·9	65·1	70·8
1136	6·8	4·7	69·2	9·7	7·4	5·1	69·0	70·1
KO 8	4·6	3·4	73·9	5·8	4·7	2·7	57·4	79·3
Mean	6·0	4·2	70	8·3	6·2	3·9	61	74
Number	16	16	16	13	13	13	13	13
S.D.	0·62	0·46	4·69	1·29	0·85	0·96	9·10	8·64
Coef. var.	10·3	10·9	6·7	15·6	13·7	24·6	14·9	11·7
S.E.	0·15	0·11	1·17	0·36	0·23	0·27	2·52	2·40
95% conf.	4·6	3·2	60	6·9	4·3	1·8	41	55
limits	7·4	5·2	80	12·5	8·1	6·0	81	93
P. africanus								
M 32363	9·6	6·1	63·5	12·4	9·0	5·8	64·5	77·4
RU 1698	9·1	6·3	69·3	13·6	10·3	6·4	62·2	66·8
1769	8·6	6·2	72·1	12·3	9·4	7·8	83·0	69·9
1785	8·1	6·0	74·2	10·7	7·9	6·1	77·2	75·6
1899	9·3	6·6	71·0	12·7	9·0	6·4	71·1	73·2
1914	9·4	6·2	66·0	12·3	9·2	6·0	65·2	76·4
1999	8·6	6·7	77·9	–	–	–	–	–
2036	8·4	6·2	73·8	11·5	9·3	7·5	80·7	74·1
2071	8·6	7·1	82·6	–	–	–	–	–
MW 45	9·4	7·0	74·4	–	–	–	–	–
59	8·4	6·8	81·0	–	–	–	–	–
160	8·8	5·7	64·8	11·5	7·9	6·3	79·8	76·5
KO 9	10·4	7·9	76·0	14·5	11·0	8·3	75·4	71·7
Mean	9·0	6·5	73	12·4	9·2	6·7	73	74
Number	13	13	13	9	9	9	9	9
S.D.	0·63	0·58	5·90	1·14	1·04	0·89	7·76	3·51
Coef. var.	7·0	8·9	8·1	9·2	10·9	13·3	10·6	4·8
S.E.	0·18	0·16	1·64	0·38	0·33	0·30	2·59	1·17
95% conf.	7·6	5·2	60	9·8	6·9	4·7	56	65
limits	10·4	7·8	86	15·0	11·5	8·7	91	82

Table 13 (*cont.*)

	max l	perp b	b/l	buc ht	mesial ht	mesial ridge	ridge / ht	max l / buc ht
P. nyanzae								
M 32236	12·2	9·5	77·9	–	13·3	11·3	85·0	–
RU 1674	11·3	8·4	74·2	16·9	10·0	7·5	75·0	66·9
1676	12·6	9·6	76·2	18·1	15·7	12·7	80·9	69·6
1717	10·9	8·2	75·2	–	–	–	–	–
1740	13·1	8·7	66·3	–	–	–	–	–
1791	11·5	9·3	80·8	–	–	–	–	–
1840	13·7	11·2	81·7	–	–	–	–	–
1889	12·8	10·0	78·1	–	–	–	–	–
1926	12·3	9·7	78·8	–	–	–	–	–
1947	12·8	10·3	80·5	18·0	15·8	12·4	78·5	71·1
1960	14·2	11·1	78·2	14·7	14·4	11·8	82·0	96·5
1982	13·6	10·2	75·0	20·7	15·1	12·0	79·5	65·7
2010	11·0	8·5	77·3	–	–	–	–	–
2024	12·9	9·4	72·8	–	–	–	–	–
2034	12·0	9·2	76·6	16·0	13·8	11·7	84·7	75·0
2048	12·4	8·9	71·8	–	–	–	–	–
2087	11·6	8·5	73·3	15·1	14·6	12·0	82·2	76·8
MW 39	11·3	7·9	69·9	–	–	–	–	–
44	13·3	9·4	70·7	–	–	–	–	–
Mean	12·4	9·4	75	17·1	14·1	11·4	81	75
Number	19	19	19	7	8	8	8	7
S.D.	0·96	0·92	4·16	–	–	–	–	–
Coef. var.	7·7	9·8	5·6	–	–	–	–	–
S.E.	0·22	0·21	0·95	–	–	–	–	–
95% conf.	10·4	7·5	66	–	–	–	–	–
limits	14·4	11·3	84	–	–	–	–	–
P. major								
M 14086	13·5	9·5	70·4	–	–	–	–	–
SO 396	14·7	11·2	76·1	21·0	17·0	15·6	91·7	70·0
404	13·1	9·0	68·7	–	–	–	–	–
Mean	13·7	9·9	72	21·0	17·0	15·6	92	70
Number	3	3	3	1	1	1	1	1

Table 14 Measurements of lower P3.

	max l	perp b	b/l	buccal ht mes	buccal ht dist	dist/mes
D. macinnesi						
M 14083*	5·6	3·7	66·1	5·1	3·6	70·5
16650	8·0	4·9	61·3	9·0	6·8	75·6
32234*	8·4	4·8	57·2	–	–	–
RU 900	6·6	4·2	63·7	7·0	5·4	77·2
1664	7·3	4·4	60·2	–	–	–
1727	7·5	4·3	57·5	–	–	–
1893	7·3	4·2	57·6	–	–	–
1898	8·3	5·1	61·5	7·0	5·5	78 6
1935	7·2	4·3	59·7	8·3	5·3	63·8
1972	8·2	4·6	56·1	8·4	5·7	67·9
MW 53	6·7	4·1	61·2	6·3	4·5	71·4
SO 405*	7·9	4·7	59·5	7·9	5·6	70·9
530*	7·4	4·5	60·8	6·6	4·8	72·7
Mean	7·5	4·5	60	7·7	5·5	72
Number	9	9	9	6	6	6
S.D.	0·61	0·34	2·40	–	–	–
Coef. var.	8·1	7·6	4·0	–	–	–
S.E.	0·20	0·11	0·80	–	–	–
95% conf.	5·6	3·7	54	–	–	–
limits	8·4	5·3	66	–	–	–
P. (R.) gordoni						
SO 377	8·5	4·6	54·2	8·1	6·6	81·5
588	10·2	5·8	56·8	8·5	–	–
948	8·5	5·3	62·4	7·7	6·5	84·4
1112	10·3	5·9	57·3	–	–	–
Mean	9·4	5·4	58	9·0	7·3	82
Number	4	4	4	3	2	2
L. legetet						
M 14284*	4·9	3·6	73·4	4·2	3·7	88·1
32227*	5·1	3·4	65·6	4·3	3·7	86·1
RU 1916	6·0	3·5	58·4	5·5	3·9	70·8
SO 386	5·5	3·9	70·9	5·3	4·6	86·7
474	6·4	3·6	56·3	6·4	4·7	73·4
525	6·6	4·0	60·6	6·9	4·6	66·6
533	6·2	4·2	67·7	6·0	4·4	73·3
1075	5·5	3·6	65·5	6·3	4·8	76·2
Mean	5·9	3·8	65	5·9	4·5	77
Number	7	7	7	7	7	7

* Not included in calculation of sample parameters.

Table 14 (*cont.*)

	max l	perp b	b/l	buccal ht mes	buccal ht dist	dist/mes
P. africanus						
M 32363	8·5	5·6	65·8	9·5	7·1	75·0
RU 1762	8·1	5·2	64·2	7·1	5·4	76·0
1955	8·1	5·1	62·9	7·4	6·0	81·1
1958	8·0	5·1	63·7	9·3	6·9	74·2
2008	9·0	5·7	63·3	–	–	–
2036	8·5	6·0	70·6	9·0	6·6	73·4
Mean	8·4	5·4	65	8·4	6·4	76
Number	6	6	6	5	5	5
P. nyanzae						
M 32235	11·6	7·0	60·3	10·0	6·5	65·0
RU 1674	8·6	6·5	75·6	11·0	6·2	56·3
1676	9·6	6·9	71·9	9·6	8·1	84·4
1711	11·3	6·8	60·2	–	–	–
1765	10·0	6·0	60·0	–	–	–
1782	11·0	6·6	60·0	11·1	7·9	71·2
1924	12·9	6·8	52·7	11·6	6·9	59·4
1947	12·2	7·3	59·8	9·4	7·1	75·5
1982	11·6	6·9	59·4	11·7	7·7	65·8
2087	11·0	6·9	62·7	9·6	7·5	78·2
Mean	11·0	6·8	63	10·5	7·2	70
Number	10	10	10	8	8	8
S.D.	1·27	0·34	6·73	–	–	–
Coef. var.	11·6	5·0	10·7	–	–	–
S.E.	0·40	0·11	2·13	–	–	–
95% conf.	8·1	6·0	48	–	–	–
limits	13·9	7·6	78	–	–	–
P. major						
M 14086	12·2	7·0	57·4	11·9	9·2	77·3
16648	13·8	8·9	64·5	–	–	–
SO 465	16·2	9·6	59·2	–	–	–
466	16·0	9·2	57·5	15·2	11·6	76·3
1114	12·2	8·2	67·2	–	–	–
1242	12·0	7·5	62·5	–	–	–
Mean	13·6	8·4	61	13·5	10·4	77
Number	6	6	6	2	2	2

Table 15 Measurements of lower P4.

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$	$\frac{P_4}{M_1}$
D. macinnesi					
M 16650	5·9	5·6	94·9	5·7	–
RU 900	4·6	5·2	113·1	4·9	84·5
1727	5·4	5·1	94·4	5·3	80·3
1758	5·2	4·7	90·5	4·9	–
1857	5·0	4·6	92·0	4·8	78·7
1882	5·6	4·4	78·6	5·0	–
1893	5·4	4·6	85·2	5·0	–
1901	6·1	4·9	80·3	5·5	87·3
1935	5·2	4·7	90·3	5·0	–
2015	5·4	5·0	92·6	5·2	83·9
MW 53	4·6	4·1	89·2	4·4	78·7
SO 378*	4·1	5·1	124·4	4·6	86·8
Mean	5·3	4·8	91	5·1	82
Number	11	11	11	11	6
S.D.	0·47	0·41	9·08	0·36	–
Coef. var.	8·9	8·5	10·0	7·1	–
S.E.	0·14	0·12	2·74	0·11	–
95% conf.	4·2	3·9	71	4·3	–
limits	6·4	5·7	111	5·9	–
P. (R.) gordoni					
SO 374	6·1	5·3	86·9	5·7	80·3
377	5·6	5·6	100·0	5·6	–
590	6·3	5·1	81·0	5·7	–
591	6·4	5·7	89·1	6·1	–
592	7·4	5·5	74·3	6·5	–
593	6·1	6·4	105·0	6·3	–
1112	6·2	6·7	108·0	6·5	–
Mean	6·3	5·8	92	6·1	80
Number	7	7	7	7	1
L. legetet					
M 14284*	4·2	4·0	95·3	4·1	–
RU 1916	4·9	4·2	85·7	4·5	–
SO 385	4·8	3·7	77·1	4·3	84·3
595	5·0	4·4	88·0	4·7	–
KO 8	4·7	4·0	85·1	4·4	83·1
Mean	4·8	4·1	84	4·5	84
Number	4	4	4	4	2

* Not included in calculation of sample parameters.

Table 15 (*cont.*)

	md	bl	$\frac{bl}{md}$	$\frac{md+bl}{2}$	$\frac{P_4}{M_1}$
P. africanus					
M 32363	6·2	6·7	108·0	6·5	82·0
RU 1706	6·4	6·7	104·8	6·6	87·0
1824	6·2	6·6	106·4	6·4	88·0
1868	6·1	6·4	104·9	6·3	–
1955	5·6	6·3	112·5	6·0	77·0
2036	5·7	6·2	108·8	6·0	77·0
2044	5·8	6·0	103·4	5·9	–
MW 56	6·0	6·6	110·0	6·3	–
Mean	6·0	6·4	108	6·3	82
Number	8	8	8	8	5
P. nyanzae					
RU 1674	6·5	7·8	120·0	7·2	86·7
1676	8·1	8·1	100·0	8·1	89·0
1678	6·9	7·2	104·3	7·1	85·5
1679	7·3	7·8	106·8	7·6	83·5
1710	7·9	7·4	93·7	7·7	85·8
1711	6·8	7·5	110·3	7·2	83·8
1716	8·2	8·4	102·2	8·3	–
1731	8·7	7·5	86·3	8·1	–
1780	6·6	7·7	116·7	7·2	80·9
1947	7·7	8·3	107·7	8·0	94·2
1982	8·6	7·7	89·4	8·2	84·5
2087	6·4	6·7	104·7	6·6	83·6
MW 55	7·0	7·8	111·4	7·4	–
Mean	7·4	7·7	104	7·6	86
Number	13	13	13	13	10
S.D.	0·81	0·45	10·07	0·53	3·67
Coef. var.	10·9	5·9	9·7	7·0	4·3
S.E.	0·22	0·13	2·79	0·15	1·16
95% conf.	5·6	6·7	82	6·4	78
limits	9·2	8·7	126	8·8	94
P. major					
M 14086	7·7	8·9	115·6	8·3	86·5
16648	9·0	9·7	107·8	9·4	84·7
SO 396	8·9	9·7	109·0	9·3	83·0
416	9·4	10·3	109·6	9·9	–
UM-P 62-06	8·5	8·7	102·2	8·6	–
62-13	8·6	9·1	105·8	8·9	90·0
62-16	7·9	9·0	113·9	8·5	84·2
66-02	7·8	9·0	115·2	8·4	–
Mean	8·5	9·3	110	8·9	86
Number	8	8	8	8	5

Table 16 Measurements of lower M1.

	md	bl mes	bl dist	bl mes / md	bl dist / bl mes	(md + bl mes) / 2
D. macinnesi						
RU 900	6·2	5·3	–	85·5	–	5·8
1727	7·2	6·0	6·1	83·2	101·7	6·6
1773	7·1	5·4	5·6	76·0	103·7	6·3
1798	6·7	5·3	5·5	79·2	103·8	6·0
1804	6·3	4·8	–	76·2	–	5·6
1849	7·0	5·4	–	77·2	–	6·2
1850	6·1	5·3	5·4	86·8	101·9	5·7
1852	6·8	5·3	5·5	78·0	103·8	6·1
1857	6·7	5·5	5·7	82·2	103·7	6·1
1901	7·0	5·5	5·7	78·6	103·7	6·3
1925	6·5	4·9	–	75·4	–	5·7
1994	6·5	5·3	–	81·6	–	5·9
2015	6·9	5·4	5·7	78·2	105·6	6·2
2065	6·7	5·4	5·5	80·6	101·9	6·1
MW 53	6·2	–	5·0	–	–	5·6
SO 378*	5·6	4·9	5·0	87·5	102·1	5·3
530*	6·0	4·9	5·1	81·7	104·1	5·5
Mean	6·7	5·3	5·6	80	103	6·0
Number	15	14	10	14	9	15
S.D.	0·35	0·28	0·28	3·54	1·26	0·29
Coef. var.	5·2	5·3	5·0	4·4	1·2	4·8
S.E.	0·09	0·07	0·08	0·95	0·42	0·08
95× conf.	5·9	4·7	5·0	73	100	5·4
limits	7·5	5·9	6·2	87	106	6·6
P. (R.) gordoni						
RU 1768	8·8	6·9	7·1	78·4	103·0	7·9
SO 374	7·9	6·2	6·2	78·5	100·0	7·1
434	7·8	5·9	6·1	75·7	103·4	6·9
445	7·7	5·9	–	76·6	–	6·8
463	8·4	6·0	6·1	71·4	101·6	7·2
507	7·6	6·0	6·0	78·9	100·0	6·8
522	8·5	6·8	6·8	80·0	100·0	7·7
904	8·3	6·2	6·4	74·7	103·2	7·2
905	8·6	6·6	6·9	76·8	104·5	7·6
Mean	8·2	6·3	6·5	77	102	7·2
Number	9	9	8	9	8	9
S.D.	0·44	0·39	0·42	2·62	1·80	0·40
Coef. var.	5·4	6·2	6·5	3·4	1·8	5·6
S.E.	0·15	0·13	0·15	0·87	0·64	0·13
95% conf.	7·2	5·4	5·5	71	98	6·3
limits	9·2	7·2	7·5	83	106	8·1

* Not included in calculation of sample parameters.

Table 16 (*cont.*)

	md	bl mes	bl dist	bl mes / md	bl dist / bl mes	(md + bl mes) / 2
L. legetet						
M 14079	5·6	4·6	4·9	82·2	106·5	5·0
RU 1984	5·7	4·6	4·7	80·7	102·2	5·2
2078	5·6	4·6	4·7	82·2	102·2	5·1
SO 376	5·6	4·3	4·5	76·9	104·7	5·0
385	5·7	4·5	4·6	79·0	102·3	5·1
386	5·6	4·2	4·1	75·0	97·6	4·9
387	6·0	4·8	5·0	80·0	104·2	5·4
425	6·0	4·8	4·9	80·0	102·2	5·4
426	5·5	4·1	4·5	74·5	109·7	4·8
435	6·1	5·1	5·1	83·6	100·0	5·6
482	5·5	4·5	4·7	81·9	104·4	5·0
534	5·6	4·4	4·6	78·5	104·6	5·0
597	6·1	5·0	5·2	82·0	104·0	5·6
598	5·5	4·1	4·3	74·5	104·8	4·8
599	5·1	4·0	4·3	78·4	107·5	4·6
900	6·1	4·6	4·7	75·4	102·2	5·4
KO 8	5·8	4·7	4·8	81·0	102·0	5·3
WF 1	6·3	5·0	5·0	79·4	100·0	5·7
Mean	5·7	4·5	4·7	79	104	5·2
Number	18	18	18	18	18	18
S.D.	0·30	0·33	0·31	2·93	2·88	0·31
Coef. var.	5·1	7·3	6·6	3·7	2·8	5·9
S.E.	0·07	0·08	0·07	0·68	0·67	0·07
95% conf.	5·1	3·8	4·0	73	98	4·5
limits	6·3	5·2	5·4	85	110	5·9
P. africanus						
M 32363	8·5	7·2	7·3	84·7	101·4	7·9
RU 1680	8·0	6·5	–	81·2	–	7·3
1706	8·0	7·1	7·4	88·8	104·2	7·6
1728	7·4	6·7	–	90·6	–	7·1
1824	7·7	6·9	–	89·5	–	7·3
1955	8·4	7·2	7·0	85·7	97·2	7·8
1980	8·3	7·2	–	86·7	–	7·8
2036	8·4	7·1	7·4	84·5	104·2	7·8
2093	8·2	6·9	–	84·2	–	7·6
SO 901	7·7	7·0	6·7	90·9	95·7	7·4
903	8·6	7·3	7·5	84·9	102·8	8·0
Mean	8·1	7·0	7·2	87	101	7·6
Number	11	11	6	11	6	11
S.D.	0·38	0·24	–	4·34	–	0·29
Coef. var.	4·7	3·4	–	5·0	–	3·8
S.E.	0·12	0·07	–	1·31	–	0·09
95% conf.	7·2	6·5	–	78	–	7·0
limits	8·8	7·5	–	97	–	8·2

Table 16 (*cont.*)

	md	bl mes	bl dist	bl mes / md	bl dist / bl mes	(md + bl mes) / 2
P. nyanzae						
RU 1674	9·1	7·4	7·9	81·3	106·8	8·3
1676	9·7	8·4	8·5	86·6	101·2	9·1
1678	9·1	7·4	7·9	81·3	106·8	8·3
1679	9·8	8·3	8·5	84·7	102·3	9·1
1710	9·2	7·5	7·6	81·5	101·3	8·4
1711	9·2	8·0	8·0	87·0	100·0	8·6
1780	9·5	8·2	8·5	86·3	103·7	8·9
1789	9·5	8·1	8·1	85·3	100·0	8·8
1818	9·5	7·8	7·9	82·2	101·2	7·7
1822	9·4	7·8	7·9	83·0	101·2	8·6
1947	9·2	7·8	8·3	84·8	107·8	8·5
1982	10·1	9·2	9·1	91·1	98·9	9·7
2000	9·6	8·3	8·5	86·4	102·3	9·0
2032	10·6	9·0	8·9	84·9	98·9	9·8
2087	8·4	7·3	7·3	86·9	100·0	7·9
Mean	9·5	8·0	8·2	85	102	8·7
Number	15	15	15	15	15	15
S.D.	0·50	0·56	0·48	2·71	2·88	0·58
Coef. var.	5·3	7·0	5·9	3·2	2·8	6·7
S.E.	0·13	0·14	0·12	0·70	0·74	0·15
95% conf.	8·4	6·8	7·2	79	96	7·5
limits	10·6	9·2	9·2	91	108	9·9
P. major						
M 14086	9·8	9·4	9·5	95·9	101·1	9·6
16648	12·1	10·0	10·4	82·7	104·0	11·1
SO 396	11·7	10·7	10·6	91·5	99·1	11·2
470	11·2	10·4	10·2	92·9	98·1	10·8
472	11·7	10·4	10·5	88·9	101·0	11·1
542	11·2	9·7	8·9	86·6	91·8	10·5
915	11·3	10·0	10·2	88·5	102·0	10·7
916	12·0	10·0	–	83·3	–	11·0
917	12·4	10·5	10·8	84·7	102·8	11·5
1113	10·7	9·5	9·8	88·9	103·2	10·1
UM-P 62-13	10·8	9·0	9·2	83·4	102·2	9·9
62-14	12·1	10·2	10·5	84·3	102·9	11·2
62-15	12·7	10·6	11·0	83·5	103·8	11·7
62-16	10·7	9·4	9·4	87·8	100·0	10·1
Mean	11·5	10·0	10·1	88	101	10·8
Number	14	14	13	14	13	14
S.D.	0·79	0·52	0·66	4·18	3·27	0·63
Coef. var.	6·9	5·0	6·6	4·7	3·2	5·8
S.E.	0·21	0·14	0·18	1·12	0·91	0·17
95% conf.	9·8	8·9	8·7	79	94	9·4
limits	13·2	11·1	11·5	97	108	12·2

Table 17 Measurements of lower M2.

	md	bl mes	bl dist	bl mes / md	bl dist / bl mes	(md + bl mes) / 2	M_2 / M_1
D. macinnesi							
M 16650	7·9	6·7	–	84·8	–	7·3	–
RU 1725	7·8	6·7	6·5	86·0	97·0	7·3	–
1726	7·8	6·6	6·5	84·7	98·5	7·2	–
1803	7·0	5·8	5·7	82·9	98·3	6·4	114·3
1844	7·0	6·2	–	88·7	–	6·6	–
1847	7·9	6·5	–	82·2	–	7·2	–
1849	8·2	6·2	6·5	75·6	104·8	7·2	–
1850	7·1	6·2	6·1	87·3	98·4	6·7	117·9
1893	7·6	6·1	6·4	80·3	104·9	6·9	–
1901	7·4	6·6	6·7	89·2	101·4	7·0	111·1
1992	7·5	5·9	5·9	78·7	100·0	6·7	–
2003	7·6	6·0	6·1	78·9	101·7	6·8	–
2015	7·8	6·6	6·8	84·6	103·0	7·2	116·1
2046	7·6	6·3	6·0	82·9	95·3	7·0	–
2053	7·0	6·0	5·9	85·8	98·4	6·5	–
MW 53	7·5	5·8	–	77·4	–	6·7	119·6
SO 378*	5·7	5·7	5·6	100·0	98·3	5·7	107·4
405*	7·2	6·3	6·5	87·5	103·2	6·8	–
530*	6·9	5·7	5·6	83·7	98·5	6·3	114·5
Mean	7·5	6·3	6·3	83	100	6·9	115
Number	16	16	12	16	12	16	5
S.D.	0·37	0·32	0·35	4·03	3·05	0·30	–
Coef. var.	4·9	5·1	5·6	4·9	3·1	4·4	–
S.E.	0·09	0·08	0·10	1·00	0·88	0·07	–
95% conf.	6·7	5·6	5·5	74	94	6·3	–
limits	8·3	7·0	7·1	92	107	7·4	–
P. (R.) gordoni							
SO 374	9·2	7·4	7·1	80·4	95·9	8·3	117·0
420	9·7	7·8	7·7	80·4	98·7	8·8	–
463	10·0	7·6	7·3	76·0	96·1	8·8	122·0
486	9·2	7·6	7·4	82·6	97·3	8·4	–
523	9·2	7·5	7·2	81·6	96·0	8·4	–
906	9·5	6·8	7·1	71·6	104·3	8·2	–
907	9·2	7·8	–	84·8	–	8·5	–
908	9·6	7·6	7·8	79·2	102·7	8·6	–
909	10·2	7·8	8·1	76·5	103·8	9·0	–
1112	9·6	8·3	8·5	86·5	102·2	9·0	–
Mean	9·5	7·6	7·6	80	100	8·6	120
Number	10	10	9	10	9	10	2
S.D.	0·36	0·38	0·49	4·4	3·55	0·29	–
Coef. var.	3·8	5·0	6·5	5·5	3·6	3·4	–
S.E.	0·11	0·12	0·16	1·40	1·18	0·09	–
95% conf.	8·7	6·7	6·7	70	92	7·9	–
limits	10·3	8·5	8·5	90	108	9·3	–

* Not included in calculation of sample parameters.

Table 17 (*cont.*)

	md	bl mes	bl dist	bl mes / md	bl dist / bl mes	(md + bl mes) / 2	M_2 / M_1
L. legetet							
M 14079	6·3	5·8	6·0	92·1	103·4	6·1	122·0
RU 1708	6·2	5·3	5·4	85·5	101·9	5·8	–
1739	6·0	5·2	5·3	86·7	101·9	5·6	–
SO 385	6·2	5·2	5·0	83·9	96·2	5·7	111·8
386	6·0	5·2	5·1	86·7	98·0	5·6	114·3
387	6·7	5·9	5·8	88·1	98·4	6·8	126·0
388	6·7	6·1	5·8	91·1	95·1	6·4	–
411	7·2	6·1	6·1	84·8	100·0	6·7	–
424	6·3	5·2	5·2	82·5	100·0	5·8	–
444	6·5	5·6	5·7	86·2	103·6	6·1	–
458	6·7	5·5	5·4	82·2	98·3	6·1	–
482	6·2	5·2	5·2	83·9	100·0	5·7	–
532	6·8	6·1	6·0	89·7	98·4	6·5	–
534	5·9	5·0	4·8	84·8	96·0	5·5	–
910	6·0	4·9	4·7	81·7	95·9	5·5	–
911	5·9	5·0	5·0	84·8	100·0	5·5	–
912	7·0	6·0	5·9	85·8	98·5	6·5	–
913	6·1	5·3	5·2	86·9	98·1	5·7	–
1098	6·2	5·4	5·4	87·0	100·0	5·8	–
KO 7	6·9	5·5	5·7	79·7	103·6	6·2	–
8	6·3	5·4	5·4	85·7	100·0	5·9	111·4
Mean	6·4	5·5	5·4	85	99	6·0	117
Number	21	21	21	21	21	21	5
S.D.	0·38	0·39	0·41	2·88	2·50	0·41	–
Coef. var.	5·9	7·1	7·6	3·4	2·5	6·9	–
S.E.	0·08	0·08	0·09	0·64	0·55	0·09	–
95% conf.	5·7	4·7	4·5	79	94	5·2	–
limits	7·1	6·3	6·3	91	104	6·8	–
P. africanus							
M 32363	10·0	8·8	8·5	88·0	96·6	9·4	119·0
RU 1680	9·5	8·0	–	84·2	–	8·8	120·0
1683	10·5	8·5	8·3	81·0	97·6	9·5	–
1706	9·8	8·3	8·2	84·7	98·8	9·1	120·0
1728	9·0	7·5	7·5	83·4	100·0	8·3	117·0
1823	9·8	8·5	8·6	86·8	101·2	9·2	–
1824	10·1	8·6	8·5	85·1	98·9	9·4	129·0
1945	9·9	7·9	7·9	79·8	100·0	8·9	–
1955	9·4	7·6	–	80·9	–	8·5	109·0
1959	9·5	8·0	7·9	84·2	98·8	8·8	–
2036	9·6	8·0	8·2	83·4	102·5	8·8	113·0
2045	9·0	7·8	7·4	86·6	94·9	8·4	–
Mean	9·7	8·1	8·1	84	99	8·8	116
Number	12	12	10	12	10	12	7
S.D.	0·43	0·41	0·42	2·49	2·18	0·38	–
Coef. var.	4·4	5·1	5·2	3·0	2·2	4·3	–
S.E.	0·13	0·12	0·13	0·72	0·67	0·11	–
95% conf.	8·7	7·2	7·1	78	94	8·0	–
limits	10·7	9·0	9·1	89	104	9·6	–

Table 17 (*cont.*)

	md	bl mes	bl dist	bl mes / md	bl dist / bl mes	(md + bl mes) / 2	M_2 / M_1
P. nyanzae							
RU 1674	10·5	8·4	9·0	80·0	107·2	9·5	115·0
1676	12·7	10·9	11·2	85·8	102·8	11·8	130·0
1678	11·4	9·3	9·5	81·5	102·1	10·4	125·0
1694	10·7	10·1	10·1	94·4	100·0	10·4	–
1695	12·7	10·7	10·4	84·3	97·2	11·7	–
1710	11·2	9·7	9·7	86·6	100·0	10·5	125·0
1734	13·0	11·1	11·3	85·4	98·3	12·1	–
1736	11·4	9·9	9·6	86·8	97·0	10·7	–
1839	12·0	10·8	–	90·0	–	11·4	–
1947	11·6	10·4	10·4	89·7	100·0	10·9	130·0
1982	13·0	11·7	11·1	90·0	94·9	12·4	128·0
2087	10·0	8·5	8·4	85·0	98·9	9·3	118·0
MB 108	11·7	11·1	–	94·9	–	11·4	–
Mean	11·7	10·2	10·1	87	100	11·0	124
Number	13	13	11	13	11	13	7
S.D.	0·97	1·01	0·93	4·44	3·33	0·93	–
Coef. var.	8·3	9·9	9·2	5·1	3·3	8·5	–
S.E.	0·27	0·28	0·28	0·23	1·00	0·26	–
95% conf.	9·6	8·0	8·0	77	93	9·0	–
limits	13·8	12·4	12·2	97	107	11·0	–
P. major							
M 14086	11·9	10·5	10·0	88·2	99·0	11·2	106·0
16648	14·8	12·7	12·8	85·8	100·9	13·8	124·0
SO 396	13·4	13·0	12·2	97·0	93·9	13·2	118·0
415	15·2	14·3	13·7	94·1	94·0	14·8	–
914	13·4	11·1	10·9	82·8	98·2	12·3	–
Mean	13·7	12·3	11·9	90	98	13·5	116
Number	5	5	5	5	5	5	3

Table 18 Measurements of lower M3.

	md	bl mes	bl dist	bl mes / md	bl dist / bl mes	(md + bl mes) / 2	M_3 / M_1
D. macinnesi							
M 16650	8·0	6·7	6·5	83·7	97·0	7·2	–
RU 1724	8·2	6·4	6·1	78·0	95·4	7·3	–
1726	8·4	6·5	6·0	77·4	92·3	7·5	–
1737	7·9	6·4	5·9	81·0	92·2	7·2	–
1738	6·8	5·0	4·5	73·5	90·0	5·9	–
1849	8·2	6·2	5·9	75·6	95·2	7·2	–
1850	7·3	–	–	–	–	–	–
1857	8·1	6·9	–	85·2	–	7·5	123·0
1901	8·2	6·7	6·1	81·7	91·0	7·5	119·0
1970	7·4	5·6	4·9	75·7	87·5	6·5	–
2015	8·7	7·2	6·7	82·7	93·1	8·0	129·0
2025	6·6	5·5	5·2	83·4	94·6	6·1	–
2079	9·1	7·0	6·6	76·9	94·3	8·1	–
MW 49	8·3	6·6	6·0	79·6	90·0	7·5	–
SO 378*	6·5	5·3	4·9	81·5	92·5	5·9	111·3
Mean	7·9	6·4	5·9	80	92	7·2	124
Number	14	13	12	13	12	13	3
S.D.	0·70	0·64	0·68	3·67	2·44	0·66	–
Coef. var.	8·8	10·0	11·5	4·6	2·7	9·3	–
S.E.	0·19	0·18	0·20	1·02	0·74	0·18	–
95% conf. limits	6·4 9·4	5·0 7·8	4·4 7·4	72 88	87 97	5·8 8·6	– –
P. (R.) gordoni							
SO 450	9·5	7·0	6·7	73·6	95·7	8·8	–
463	11·9	8·3	7·8	69·8	94·0	10·1	140·2
464	10·3	6·9	6·7	67·1	97·2	10·1	–
921	11·7	8·7	8·0	74·4	91·9	10·2	–
1112	11·1	8·3	–	74·7	–	9·7	–
Mean	10·9	7·8	7·3	72	94	9·8	140
Number	5	5	4	5	4	5	1
L. legetet							
RU 1708	6·3	5·0	4·8	79·4	96·0	5·7	–
SO 387	6·5	5·1	4·5	78·4	88·2	5·8	118·4
388	7·4	6·2	–	83·7	–	6·8	–
444	7·3	5·5	5·3	75·3	96·4	6·4	–
481	6·5	5·2	4·4	80·0	84·6	5·9	–
532	6·8	6·0	5·6	88·2	93·4	6·4	–
918	6·8	5·9	5·5	86·7	93·2	6·4	–
919	7·7	5·9	5·6	76·6	95·0	6·8	–
KO 6	6·6	5·6	5·2	84·9	93·9	6·1	–
Mean	6·9	5·6	5·1	82	92	6·3	118
Number	9	9	8	9	8	9	1
S.D.	0·48	0·43	0·48	4·57	3·93	0·41	–
Coef. var.	6·9	7·7	9·4	5·6	4·3	6·5	–
S.E.	0·16	0·14	0·17	1·52	1·39	0·14	–
95% conf. limits	5·8 8·0	4·6 6·6	4·0 6·2	72 92	83 101	5·4 7·2	– –

Table 18 (*cont.*)

	md	bl mes	bl dist	bl mes / md	bl dist / bl mes	(md + bl mes) / 2	M_3 / M_1
P. africanus							
M 14087	12·0	9·5	8·8	79·2	92·6	10·8	–
32363	11·3	9·0	7·9	79·7	97·8	10·2	129·0
RU 1706	11·5	8·3	7·9	72·2	87·8	9·9	130·0
1728	10·2	8·4	8·1	82·4	96·4	9·3	131·0
1820	10·9	8·7	8·3	79·8	95·4	9·8	–
1855	10·0	8·1	7·8	81·0	95·8	9·0	–
1927	10·3	9·0	8·6	87·5	95·6	9·7	–
1931	11·5	8·8	8·3	76·6	94·4	10·2	–
Mean	11·0	8·7	8·2	80	94	9·8	130
Number	8	8	8	8	8	8	3
S.D.	0·73	0·45	0·36	5·34	3·09	0·66	–
Coef. var.	6·6	5·2	4·4	6·8	3·3	6·7	–
S.E.	0·26	0·16	0·13	1·89	1·09	0·23	–
95% conf.	9·3	7·6	7·3	66	87	8·2	–
limits	12·7	9·8	9·1	92	101	11·4	–
P. nyanzae							
RU 1674	12·0	9·2	9·2	76·7	100·0	10·6	127·8
1676	14·1	12·1	11·5	85·8	95·0	13·1	144·0
1678	13·5	10·2	9·3	75·6	91·2	11·1	133·9
1735	13·7	12·1	11·3	88·4	93·4	12·9	–
1764	14·8	11·6	10·4	78·4	89·7	13·2	–
1923	14·3	10·9	10·2	76·3	93·6	12·6	–
1947	14·0	11·3	10·7	80·7	94·8	12·7	149·5
1982	15·3	12·7	11·5	83·0	90·6	13·0	134·1
2087	11·3	9·4	8·4	83·2	89·4	10·4	131·8
Mean	13·6	11·1	10·3	81	93	12·2	137
Number	9	9	9	9	9	9	6
S.D.	1·28	1·23	1·11	4·52	3·35	1·14	–
Coef. var.	9·4	11·1	10·8	5·58	3·6	9·3	–
S.E.	0·43	0·41	0·37	1·51	1·12	0·38	–
95% conf.	10·6	8·3	7·7	70	85	9·6	–
limits	16·6	13·9	12·9	92	101	14·8	–
P. major							
M 16648	18·1	13·2	11·3	72·9	85·6	15·7	141·5
32237*	16·5	13·5	12·2	81·8	90·4	15·0	–
SO 396	17·3	14·2	12·1	82·1	85·3	15·8	141·0
920	16·8	13·1	12·2	77·9	93·2	15·0	–
Mean	17·4	13·5	11·9	78	88	15·5	141
Number	3	3	3	3	3	3	2

* Not included in calculation of sample parameters.

Table 19 Measurements of upper and lower dp3–dp4.

		md	bl	bl dist	bl/md	buc ht	bl dist/bl mes
Upper dp3–dp4							
D. macinnesi							
RU 1790	dp^4	4·9	5·8	–	118·2	–	–
2057	dp^4	4·6	5·8	–	125·9	–	–
P. (R.) gordoni							
SO 89	dp^3	4·6	6·2	–	134·8	4·8	–
945	dp^4	6·3	7·8	–	124·0	–	–
P. (R.) vancouveringi							
RU 1778	dp^4	6·3	5·4	–	85·7	–	–
L. legetet							
SO 536	dp^3	3·3	4·3	–	130·2	–	–
	dp^4	4·2	5·3	–	126·2	–	–
1095	dp^4	4·5	5·0	–	111·1	–	–
P. africanus							
M 32238	dp^4	6·5	7·5	–	115·2	–	–
RU 1919	dp^3	3·9	5·4	–	138·4	–	–
	dp^4	5·4	6·0	–	111·1	–	–
P. nyanzae							
RU 1693	dp^4	7·0	8·2	–	117·1	–	–
1803	dp^3	5·8	6·5	–	112·0	–	–
	dp^4	6·8	7·6	–	111·8	–	–
2031	dp^3	6·0	7·4	–	123·2	–	–
	dp^4	7·9	9·2	–	116·0	–	–
P. major							
SO 397	dp^4	8·9	9·9	–	111·2	–	–
542	dp^3	7·0	7·3	–	104·3	–	–
	dp^4	9·1	9·4	–	103·3	–	–
1101	dp^4	9·1	10·3	–	113·3	–	–
Lower dp3–dp4							
D. macinnesi							
M 16381	dp_4	5·9	3·8	4·1	64·4	–	107·9
P. (R.) gordoni							
SO 540	dp_4	8·1	5·2	5·6	64·3	–	107·7
923	dp_4	7·5	5·7	6·1	76·2	–	107·1
924	dp_4	7·4	4·7	4·9	63·5	–	104·2
925	dp_4	7·3	4·5	4·9	61·6	–	109·0
L. legetet							
M 14080	dp_3	4·7	3·1	–	66·0	–	–
	dp_4	5·0	3·9	4·2	78·1	–	107·8
SO 455	dp_4	4·9	3·5	3·7	71·5	–	105·5
1073	dp_3	4·7	3·2	–	68·2	4·5	–
	dp_4	5·4	3·8	4·2	70·4	–	110·6
1096	dp_3	4·2	2·5	–	59·6	–	–
1097	dp_3	4·0	2·6	–	65·0	–	–
KO 11	dp_3	4·8	3·3	–	68·8	4·0	–

Table 19 (*cont.*)

		md	bl	bl dist	bl/md	buc ht	bl dist/bl mes
Lower dp3–dp4 (*cont.*)							
P. africanus							
RU 1865	dp_4	6·9	5·0	5·4	72·5	–	108·0
2093	dp_3	5·9	4·6	–	78·0	–	–
	dp_4	6·5	5·2	–	80·0	–	–
P. major							
SO 451	dp_4	10·6	7·3	7·7	68·9	–	105·2
542	dp_3	8·3	–	–	–	–	–
	dp_4	9·3	6·9	7·5	74·2	–	108·8
589	dp_3	8·5	5·7	–	67·1	7·5	–
922	dp_4	9·4	7·6	7·0	80·9	–	92·0
RU 1767	dp_4	10·5	8·0	8·6	76·2	–	107·3
MO 26	dp_3	8·1	–	–	–	–	–
	dp_4	8·2	6·6	6·8	80·4	–	103·1
UM-P 62-13	dp_3	8·5	–	–	–	–	–
	dp_4	9·8	7·8	–	79·5	–	–

Table 20 Measurements of upper di1–di2.

		md	bl	bl/md	buc ht
D. macinnesi					
RU 1869	di^2	1·9	2·1	110·5	3·5
1903	di^2	1·6	1·8	107·8	3·8
SO 1238	di^2	1·5	2·0	133·3	3·6
P. (R.) gordoni					
SO 575	di^2	2·7	2·8	103·8	4·3
L. legetet					
SO 564	di^1	4·4	2·7	61·4	–
1133	di^1	4·2	2·6	62·0	–

Table 21 Measurements of upper and lower dc.

	max l	perp b	b/l	buc ht
Upper dc				
D. macinnesi				
RU 1888	4·5	3·4	75·6	5·5
P. (R.) gordoni				
SO 577	5·3	4·4	83·0	5·8
578	5·5	4·3	78·2	5·8
L. legetet				
SO 460	4·6	3·8	82·6	4·7
566	4·0	3·3	82·5	3·9
P. nyanzae				
RU 2031	5·8	4·4	75·9	–
P. major				
M 32228	7·1	5·8	81·6	–
SO 371	8·4	6·6	78·6	9·4
542	8·1	5·8	71·6	9·4
Lower dc				
D. macinnesi				
RU 1887	3·8	2·6	68·4	4·8
P. africanus				
RU 1787	5·5	4·4	80·0	7·8
P. nyanzae				
RU 1710	6·0	4·1	68·3	–
P. major				
SO 542	7·5	5·0	66·6	–
MO 26	7·0	4·7	67·2	–
UM-P 62-13	7·5	5·0	66·7	–

Table 22 Measurements of specimens from Fort Ternan.

		md	bl	$\frac{bl}{md}$
P. africanus				
KNM-FT 16	M^1 or M^2	7·7	9·7	126·0
KNM-FT 29	P^3	5·7	9·2	161·4
P. nyanzae				
KNM-FT 28	C_1	12·5	8·8	70·4
KNM-FT 34	M_3	12·3	10·2	82·9
KNM-FT 35	P_3	13·1	7·4	56·5
KNM-FT 39	C^1	15·5	11·7	75·5
KNM-FT 40	M_3	13·0	10·7	82·3
KNM-FT 49	I^1	9·9	6·8	68·7
L. legetet				
KNM-FT 11	I^1	6·2	4·2	67·7
KNM-FT 14	M_1	6·0	4·1	68·4
KNM-FT 15	C^1	7·5	5·8	77·3
KNM-FT 17	M_1	6·3	5·2	82·5
KNM-FT 18	P_4	4·3	3·8	88·4
KNM-FT 19	M^3	4·8	6·4	133·3
KNM-FT 20–24	C_1	5·6	3·7	66·1
	P_3	5·6	3·8	67·8
	P_4	4·7	4·1	87·2
	M_1	6·2	4·8	77·4
	M_2	7·0	5·3	75·6
	M_3	6·4	4·9	76·5
KNM-FT 25	I_2	3·1	4·3	138·5

Bivariate plots

Figures 7–24, p. 176–191, show the length and breadth dimensions of all the species of East African Miocene apes. In every case the mesiodistal length, or maximum length in the case of the Cs and P_3, is along the horizontal axis, and buccolingual breadth, or perpendicular breadth, is along the vertical axis. The symbols are as follows:

- × *Dendropithecus macinnesi*
- ⊘ *Proconsul* (*Rangwapithecus*) *gordoni*
- ⊗ *P.* (*R.*) *vancouveringi*
- □ *Limnopithecus legetet*
- ● *Proconsul africanus*
- ○ *P. nyanzae*
- ■ *P. major*
- ◎ *P. nyanzae* from Fort Ternan
- ⊡ *L. legetet* from Napak
- ⊙ *L. legetet* from Fort Ternan

Specimens of uncertain affiliation are denoted by a letter signifying the sites of origin. These are as follows:

L	Losidok
mb	Maboko Island
S	Songhor
FT	Fort Ternan
UM	Uganda

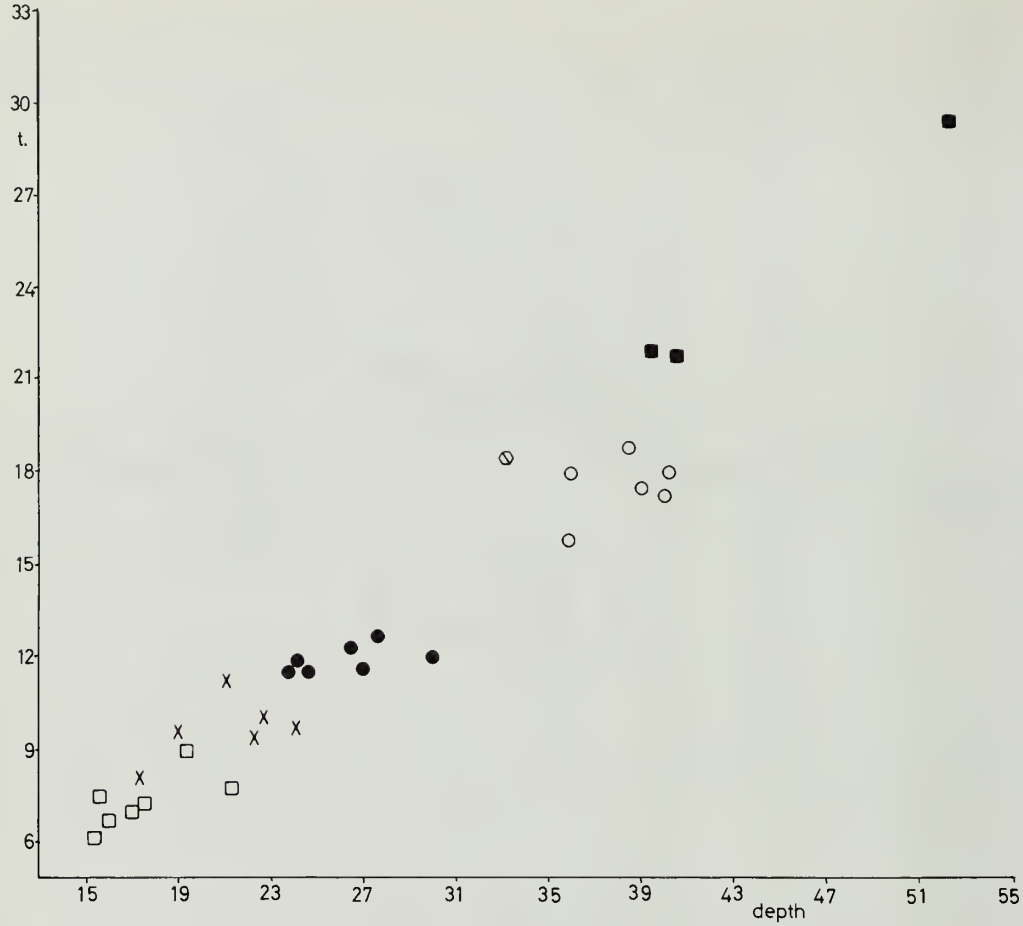


Fig. 7 Bivariate plot of symphysis.

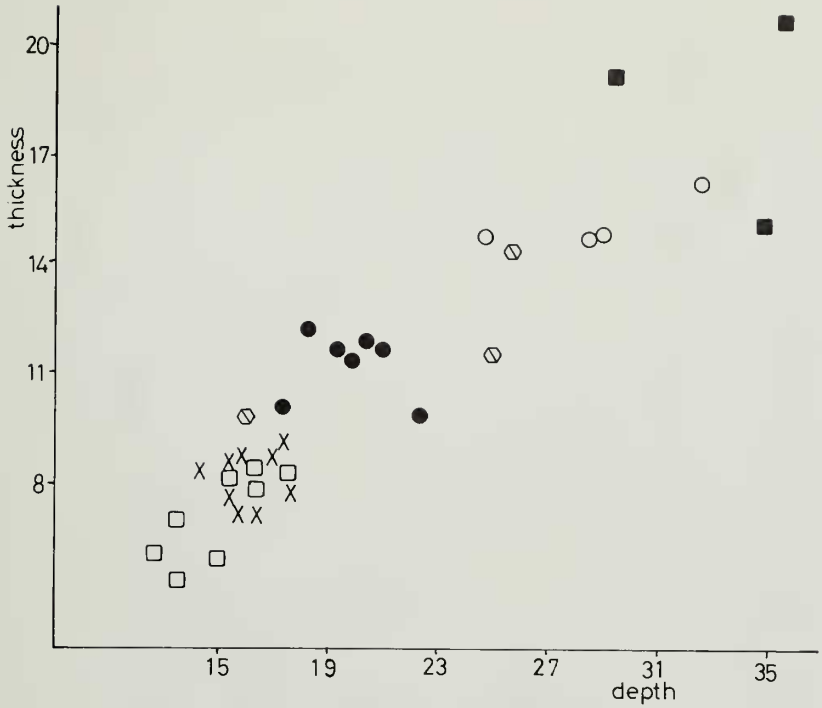


Fig. 8 Bivariate plot of mandible at M_2.

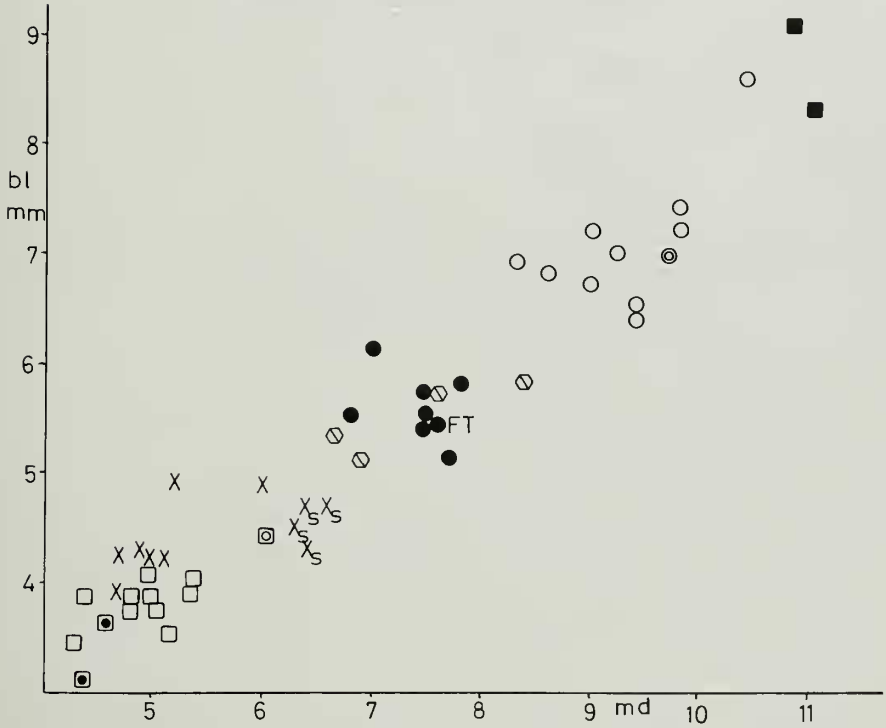


Fig. 9 Bivariate plot of I^1.

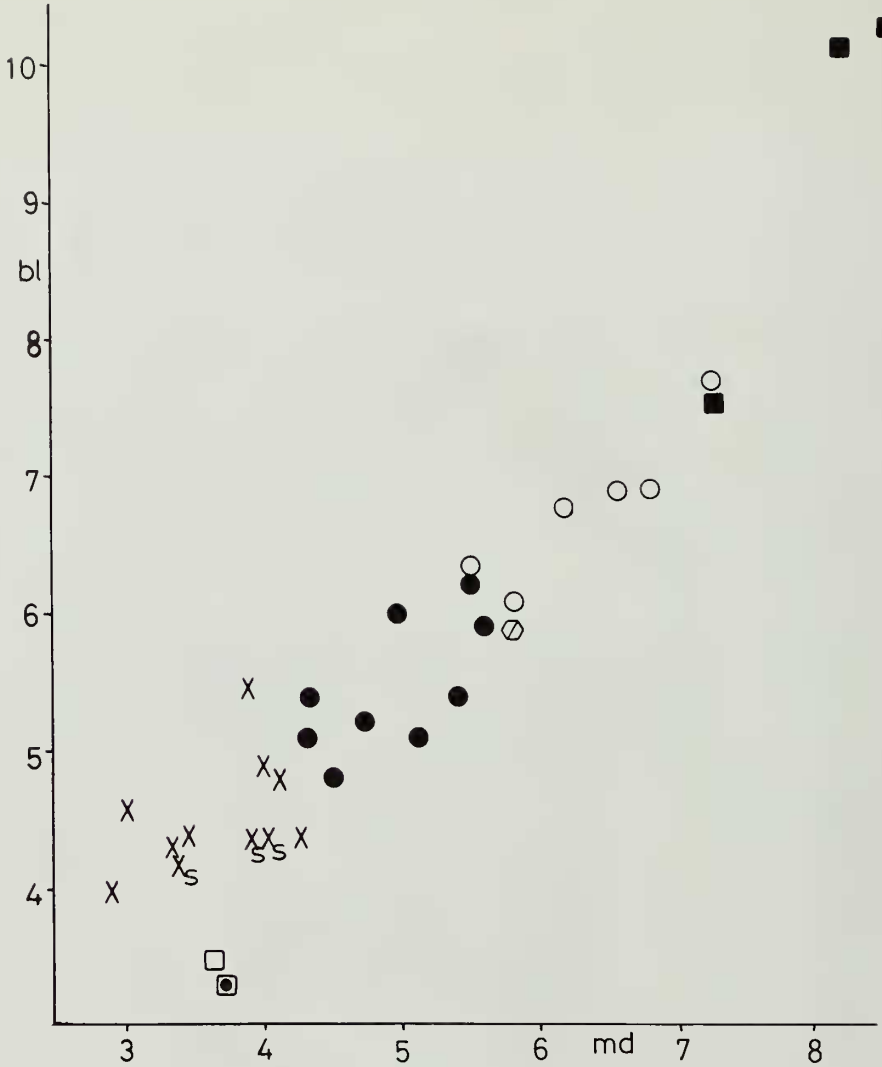


Fig. 10 Bivariate plot of I^2.

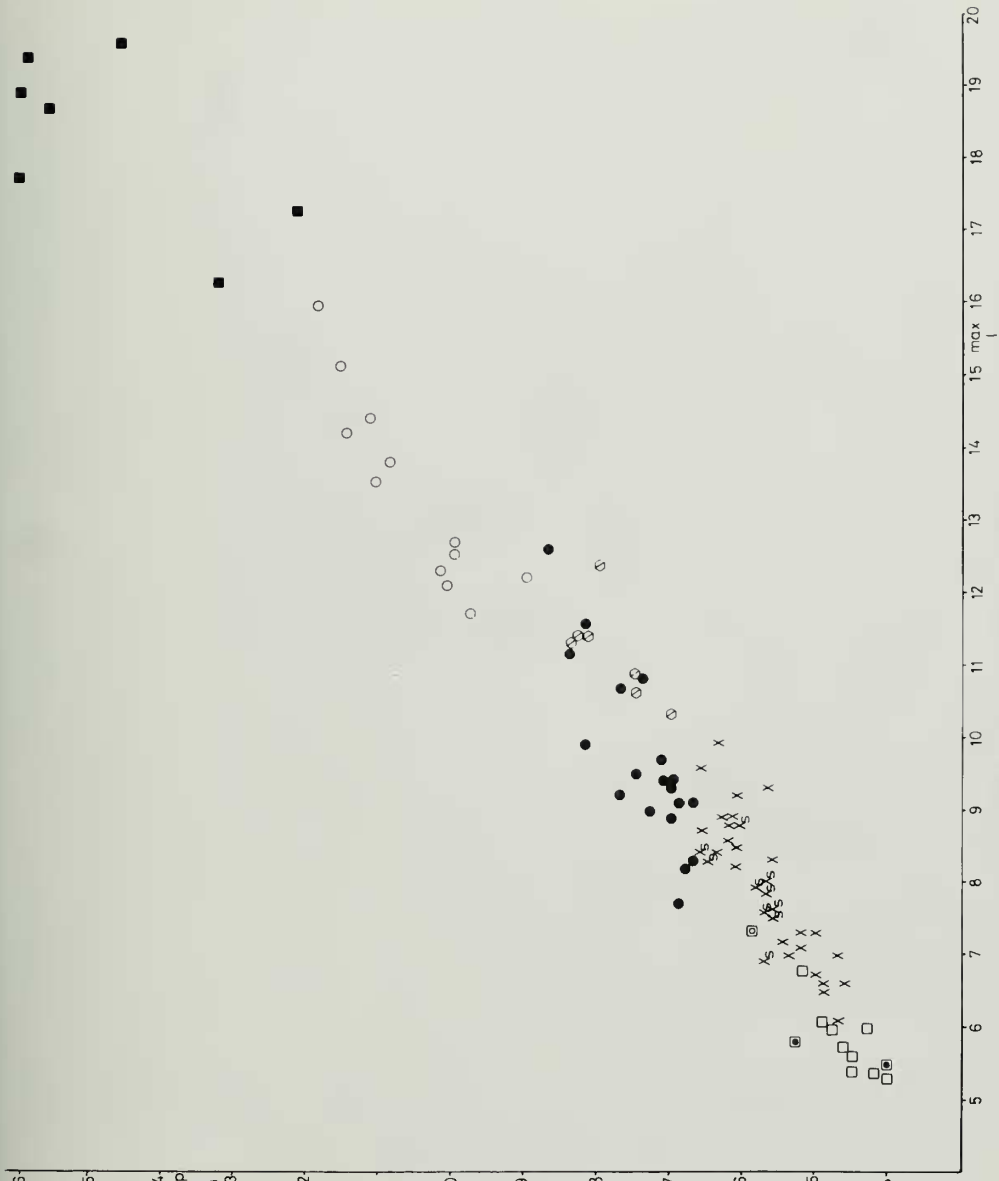


Fig. 11 Bivariate plot of upper C.

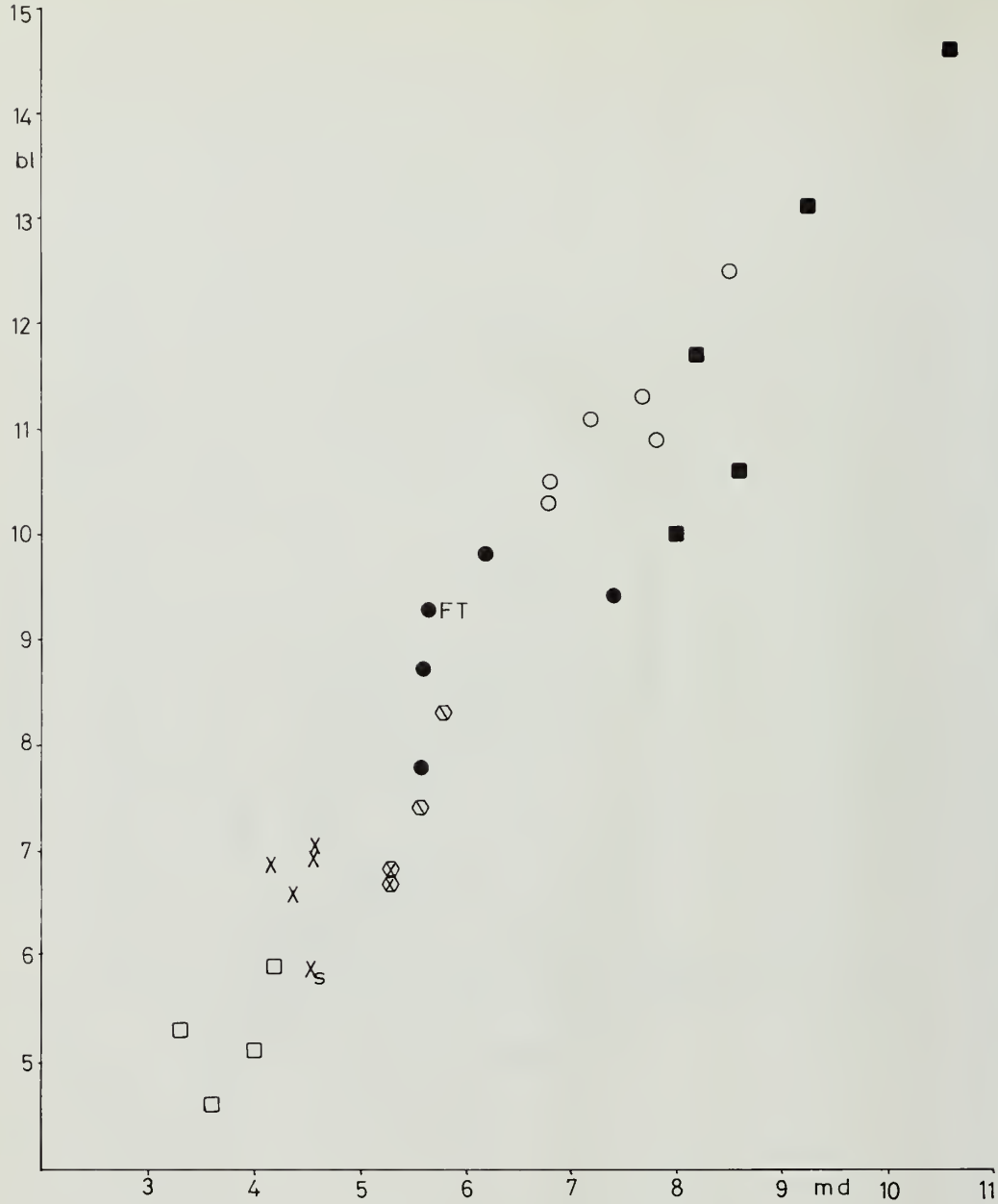


Fig. 12 Bivariate plot of P^3.

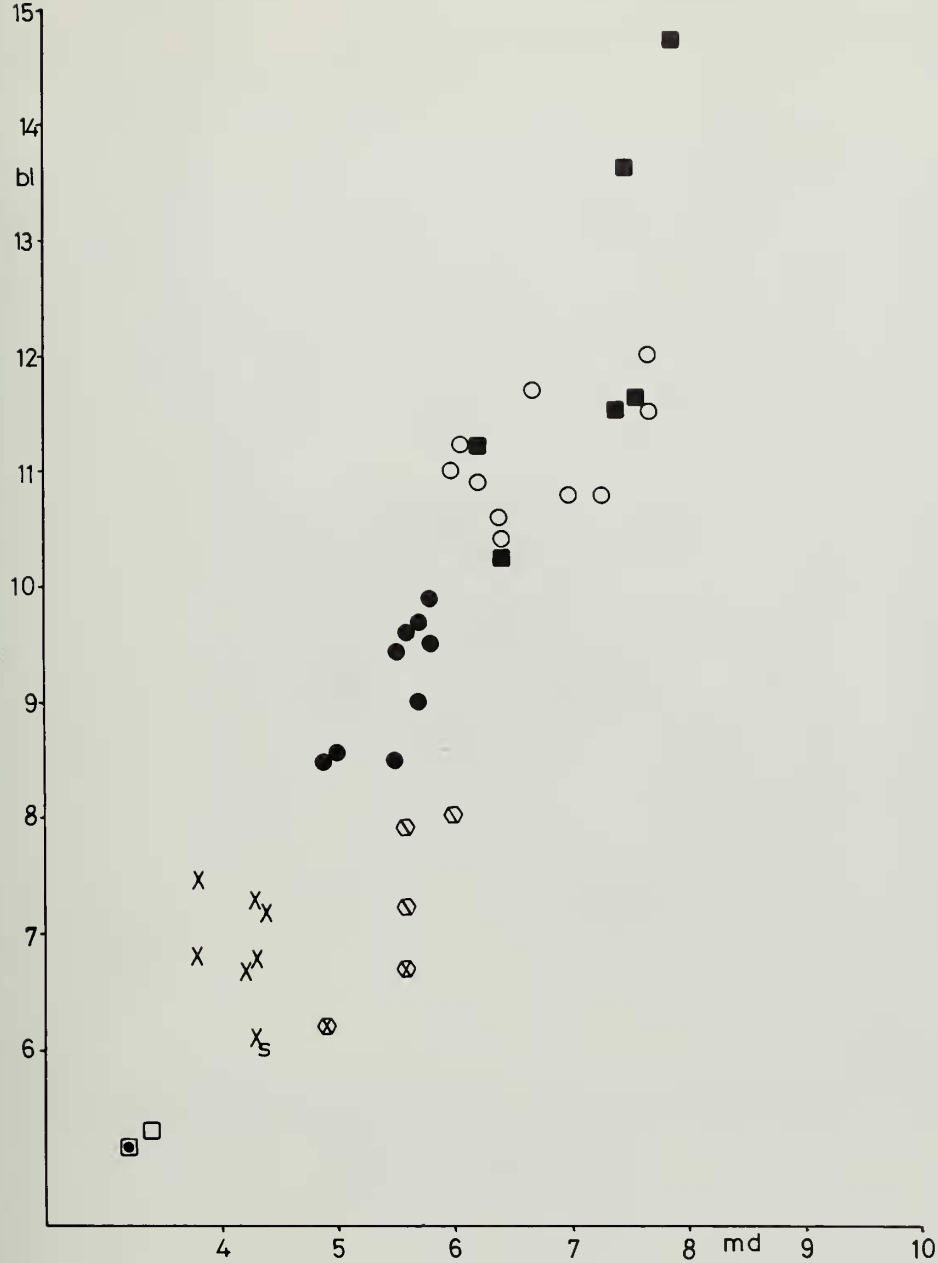


Fig. 13 Bivariate plot of P^4.

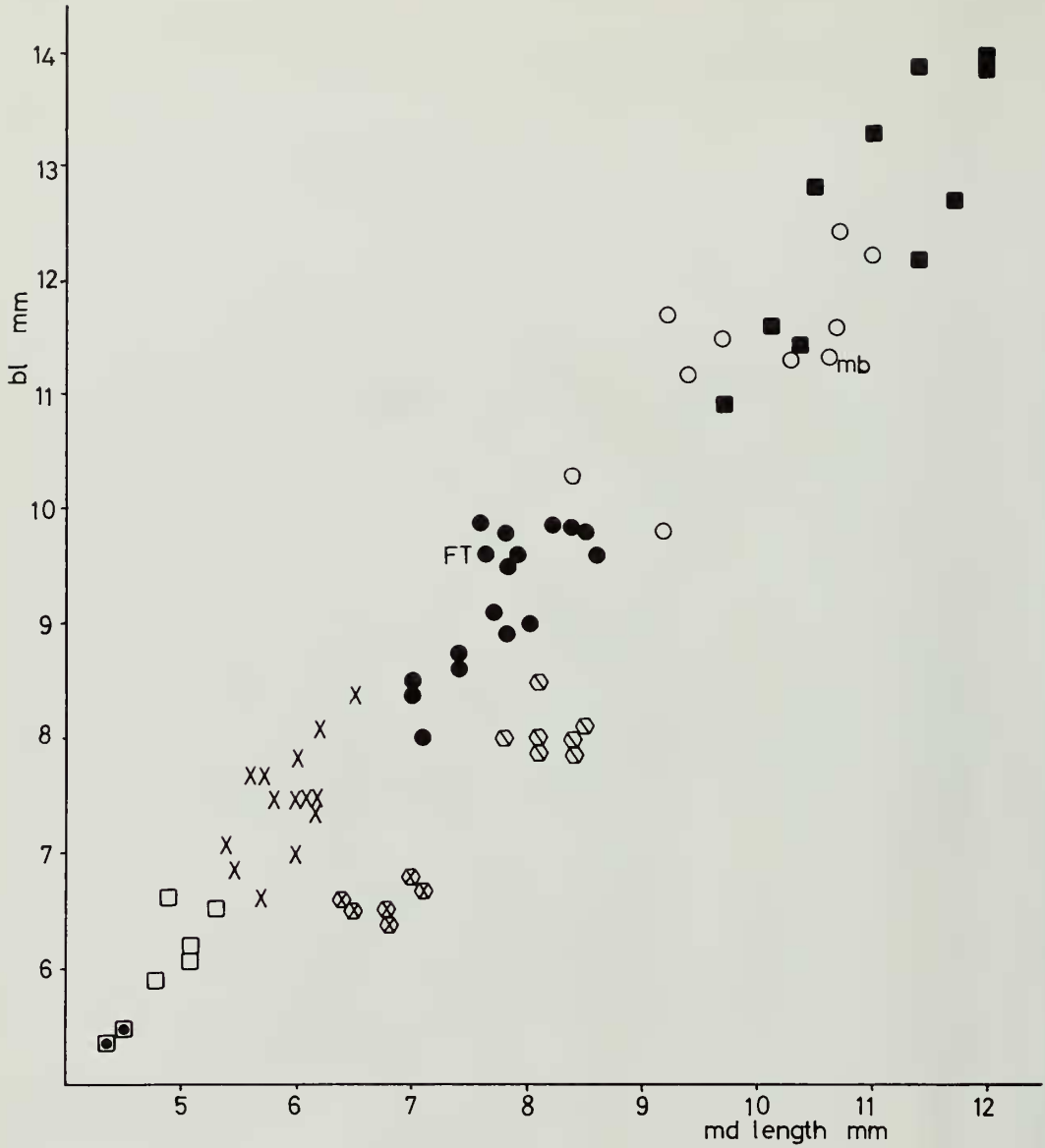


Fig. 14 Bivariate plot of M^1.

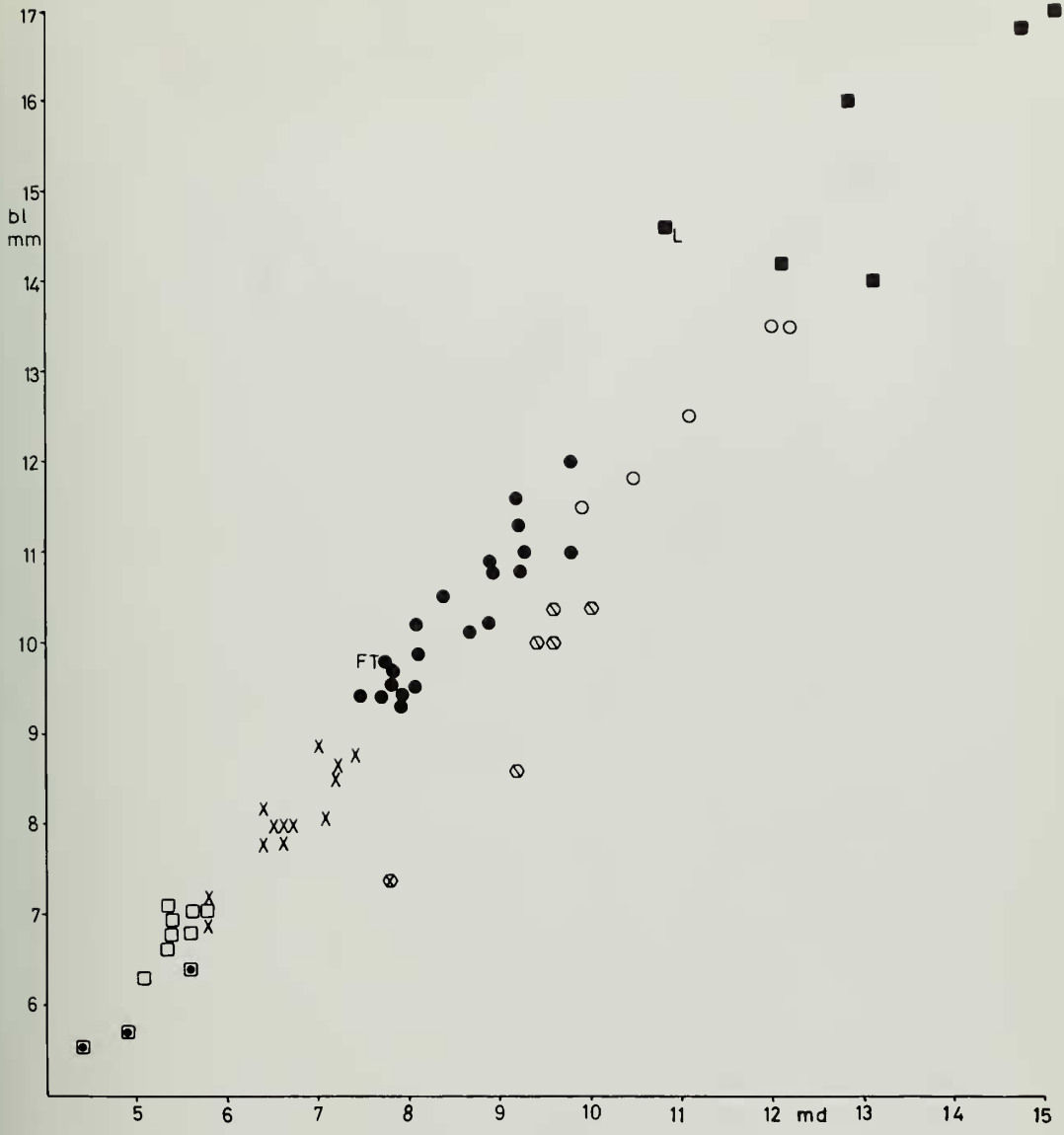


Fig. 15 Bivariate plot of M^2.

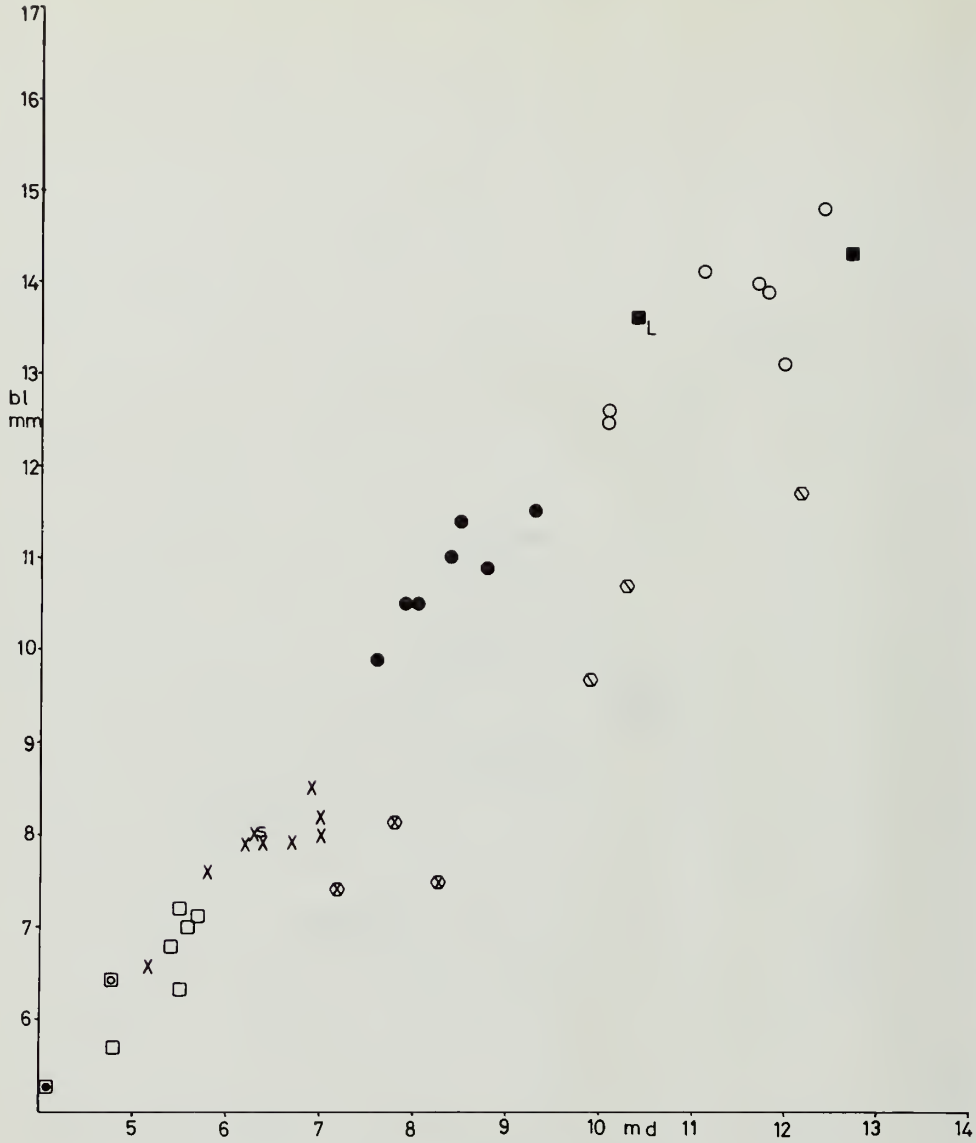


Fig. 16 Bivariate plot of M^3.

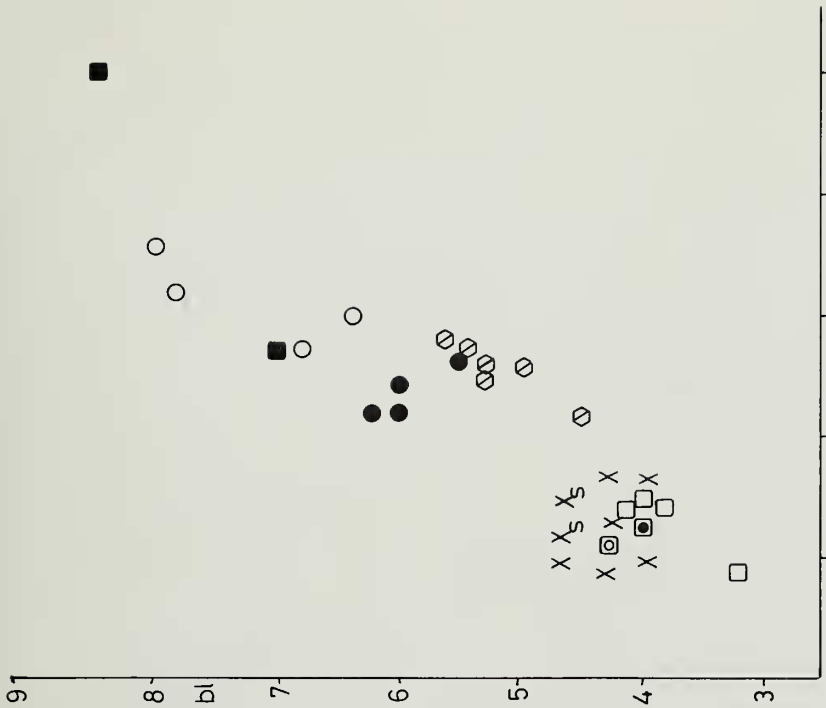


Fig. 17 Bivariate plot of I_1.

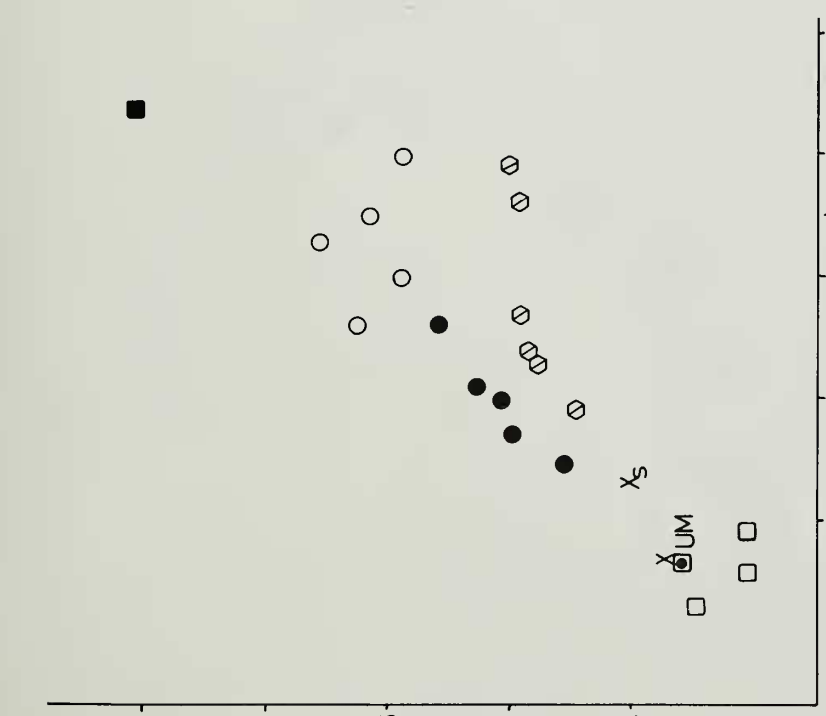


Fig. 18 Bivariate plot of I_2.

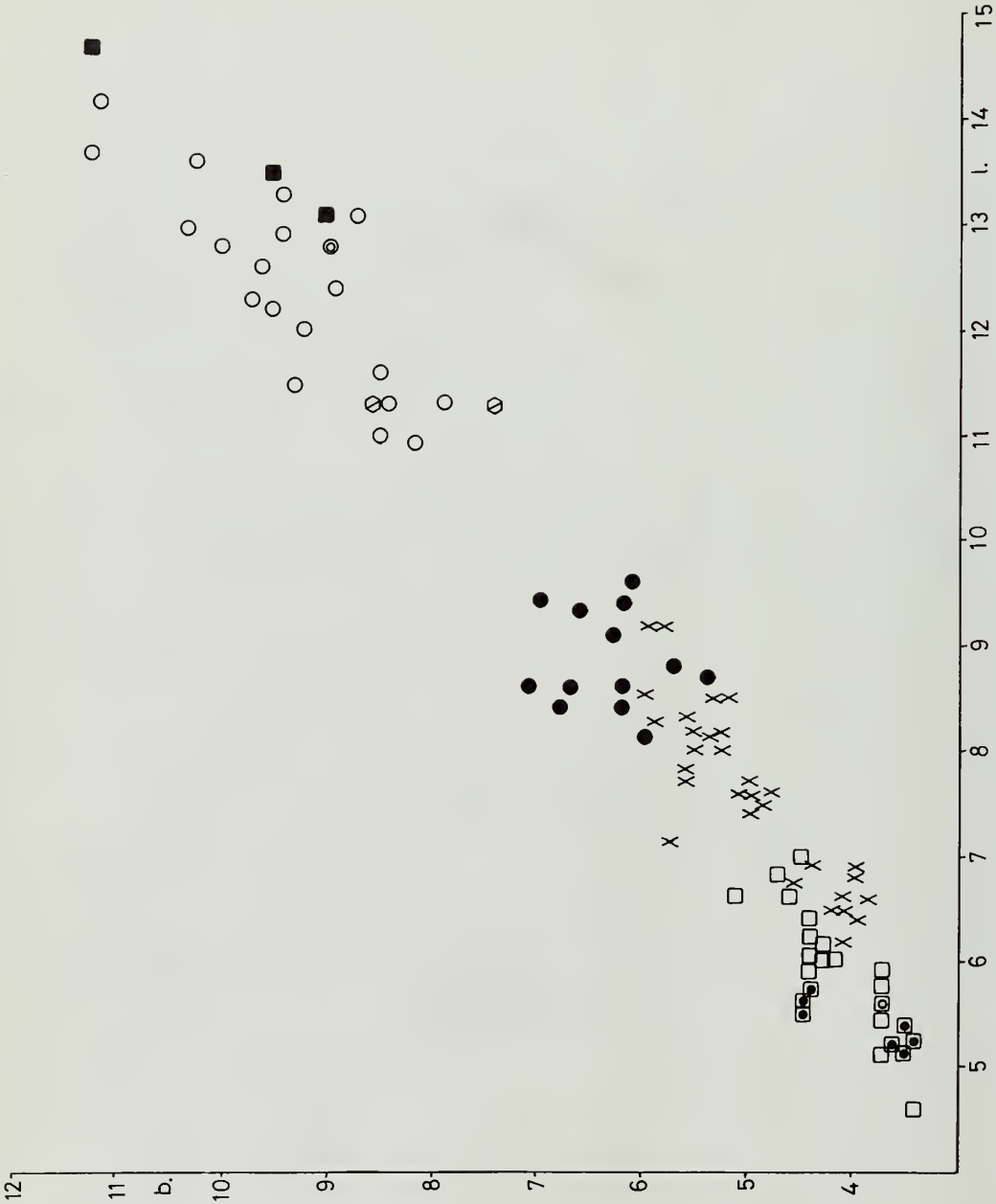


Fig. 19 Bivariate plot of lower C.

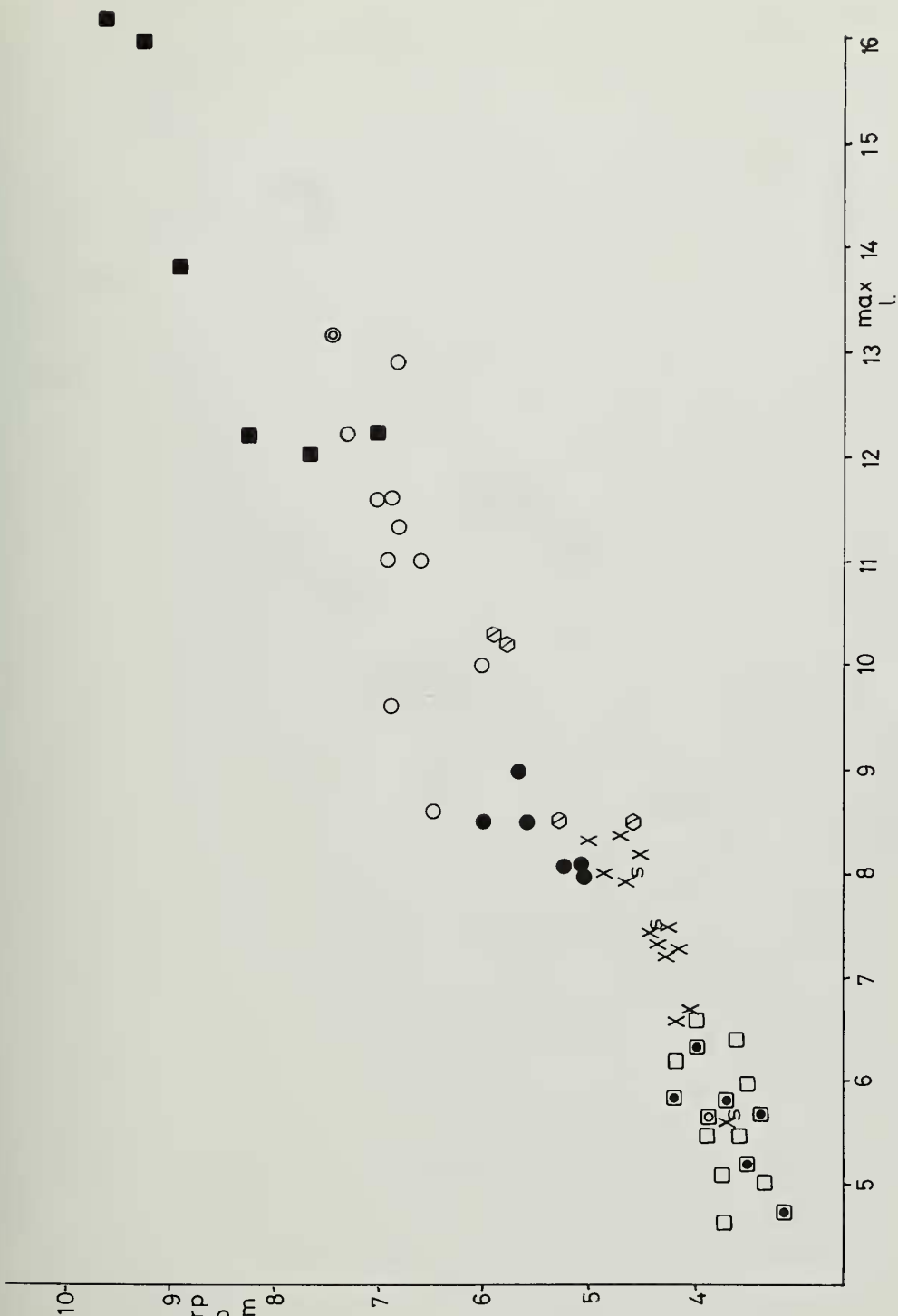


Fig. 20 Bivariate plot of P_3.

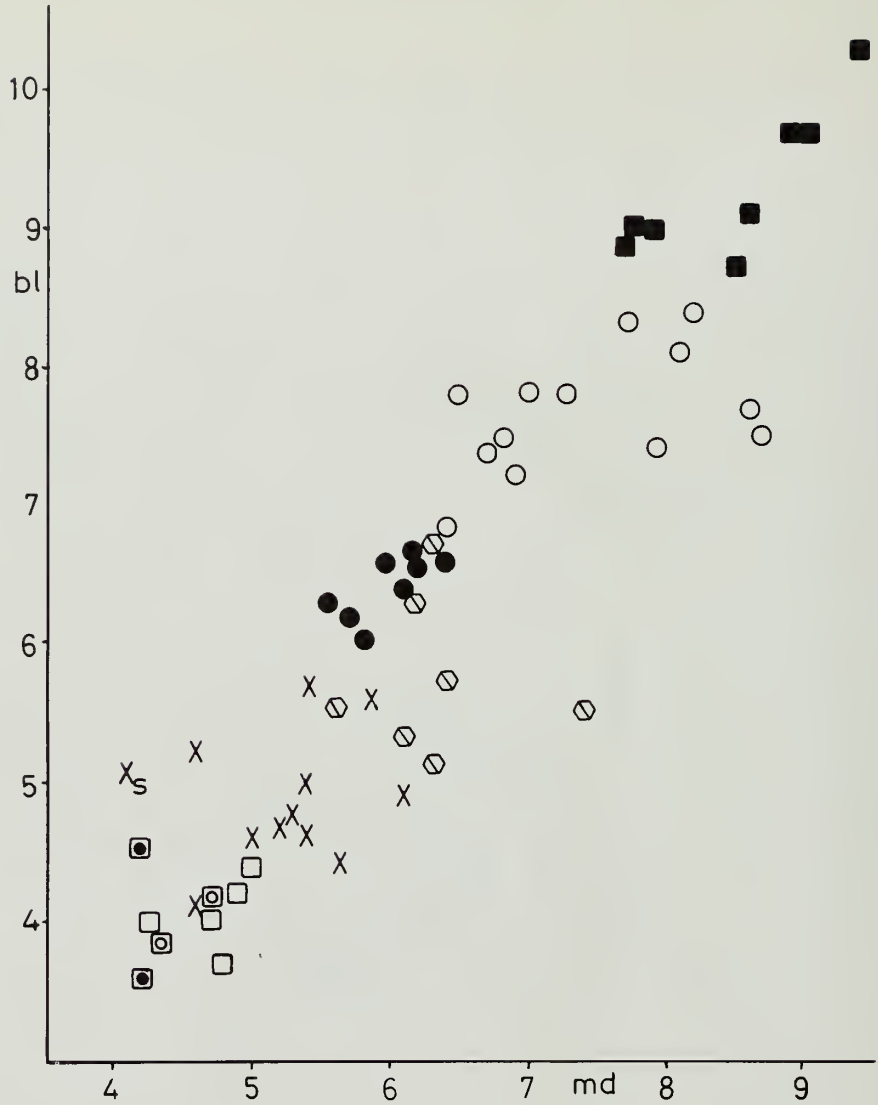


Fig. 21 Bivariate plot of P_4.

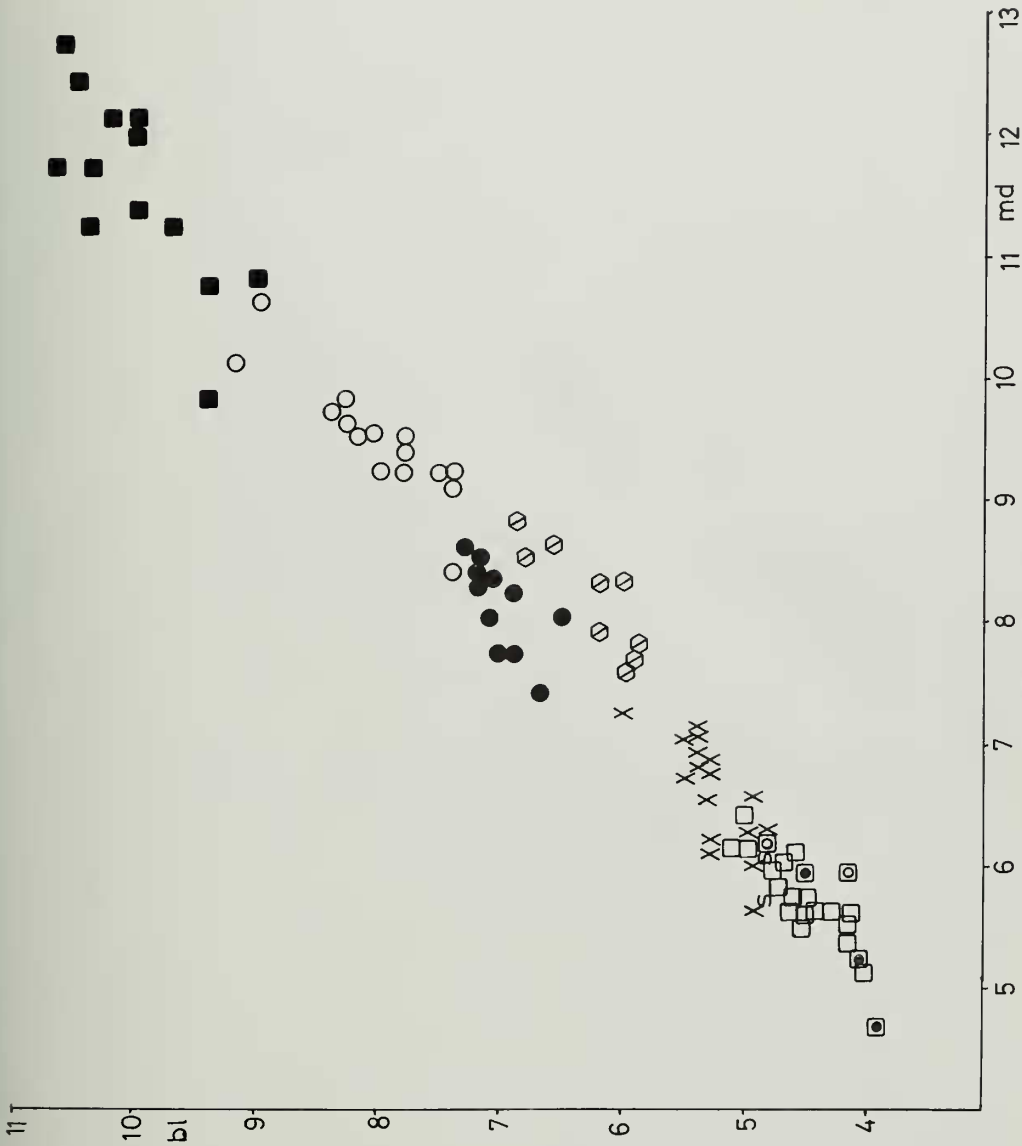


Fig. 22 Bivariate plot of M_1.

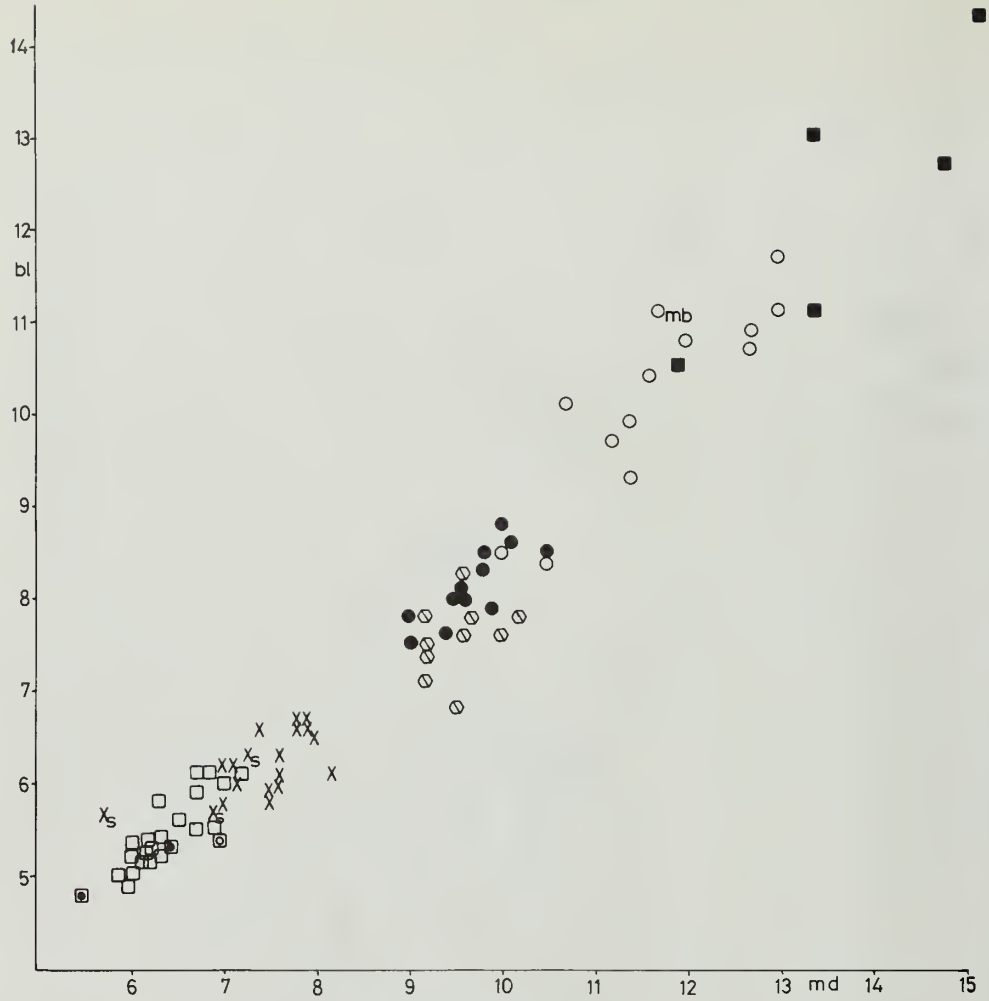


Fig. 23 Bivariate plot of M_2.

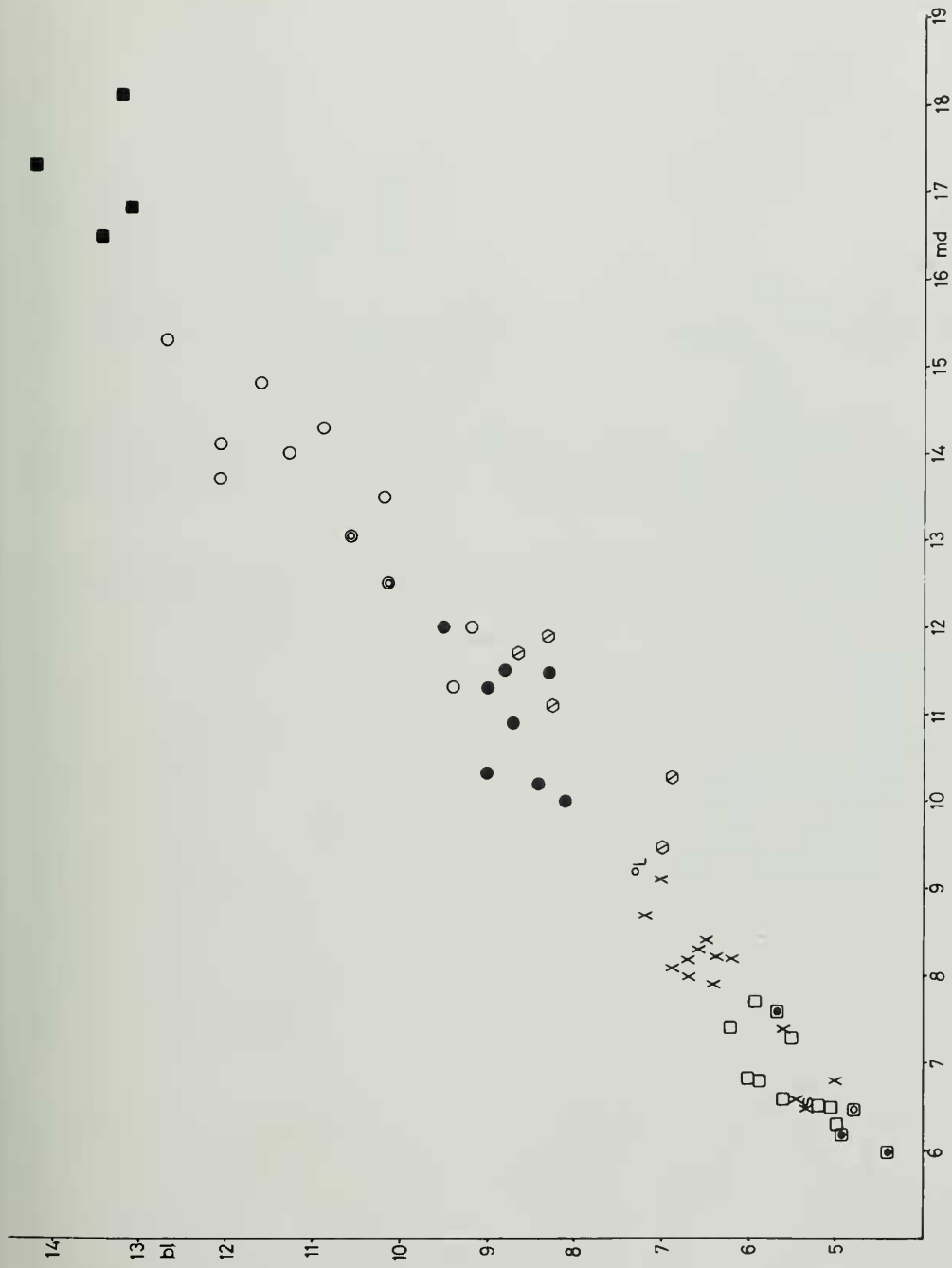


Fig. 24 Bivariate plot of M_3.

Morphological comparison of fossil and modern apes

Seven species of fossil ape are recognized from the Miocene of East Africa (Clark & Leakey 1951; Simons & Pilbeam 1965; Pilbeam 1969; Andrews 1970, 1974; Andrews, Simons & Pilbeam 1977). Six of these are placed here in two genera of the Dryopithecinae (Pongidae), *Proconsul* and *Limnopithecus*. The former is further divided into two subgenera, *P.* (*Proconsul*) and *P.* (*Rangwapithecus*), and five species, while the latter is restricted to one species, *Limnopithecus legetet*. The seventh species was formerly included also in *Limnopithecus*, but it has now been transferred to a newly-named genus, *Dendropithecus*, which is classified with the Hylobatidae.

The closest relatives to the East African fossil apes are two groups in the Oligocene of Egypt and the Middle Miocene of Europe and Asia. Comparison with the Oligocene forms is here restricted to *Aegyptopithecus zeuxis* and *Propliopithecus* species (Schlosser 1911; Simons 1965). The European Miocene apes comprise the dryopithecines *Dryopithecus fontani* and *D. laietanus* and the hylobatids *Pliopithecus antiquus* and *P. vindobonensis* (Lartet 1856; Zapfe 1960; Simons & Pilbeam 1965). The two species of *Pliopithecus* will be considered here as one morphological unit, and *D. laietanus* will be ignored as there are so few specimens representing it. From Greece there is the recently-described *Dryopithecus macedoniensis* (de Bonis *et al.* 1974). Two species of *Sivapithecus* are known from Asia, *S. sivalensis* and *S. indicus* (Simons & Pilbeam 1965).

A summary of some of the morphological features distinguishing the fossil and modern ape species is given in Table 23, p. 200–1. This list is by no means exhaustive, but it does include many of the points of difference between the fossil and modern species and also between the fossil species themselves. These points are commented on in the following sections which follow the headings of the table fairly closely.

Maxilla and premaxilla. The premaxilla in modern pongids is relatively long. In the fossil pongids it is very much shorter, and the index values for naso-alv. length are less than half those of modern pongids (Table 23, no. 1). It seems that the larger fossil species have relatively higher values of this index, presumably an allometric relation, but unfortunately there are too few specimens measurable for this feature to establish the presence of such a relation. *P.* (*R.*) *gordoni* has a lower index than the similar-sized *P. africanus*, and this might be correlated with the narrower incisors of the former. It is very possible that, when more specimens are found, *P.* (*R.*) *gordoni* will be found to have a different allometric size relation to the species of *P.* (*Proconsul*). In the hylobatids, *Dendropithecus macinnesi* has lower index values than *Pliopithecus* spp., and both are generally lower than modern gibbons.

The height of the zygomatic process is directly correlated with facial height in modern pongids. It varies in its position over the molar teeth from M^1 to M^3, and it also varies both in position and in height with age of the individual. Zygomatic width does not appear highly correlated with zygomatic height: in hylobatids the siamangs tend to have more widely flaring zygomatic arches combined with relatively low zygomatic heights, while gibbons have higher, narrower zygomatic regions, as do pongids. Of the fossil pongids, *P.* (*Proconsul*) appears to be at least as variable as modern apes in this feature. The few specimens of *P.* (*Rangwapithecus*) differ from both in having low and more widely flaring zygomatic processes, more like the condition in the siamang. In all cases the process is above either M^1 or M^2, but in *P. africanus* more of the specimens have the M^1 condition while in *P. nyanzae* more have the M^2 position.

The alveolar processes of the maxilla are long in modern pongids and they are often continued posteriorly beyond M^3 as tuberosities. The length of the tuberosity in absolute terms is greatest in gorillas, intermediate in chimpanzees, and least in the orang-utan and hylobatids. Relative to the length of the tooth row, however, the tuberosity is extremely small in the orang-utan and longer in the chimpanzees. The position of the greater palatine foramina is variable within a single species, varying from a position 7 mm beyond M^3 to opposite the middle of M^3 in gorillas of both sexes. It is set more posteriorly in the gorilla than the chimpanzee, in which it is placed no more than 3–4 mm beyond the M^3 at maximum. In the fossil apes the alveolar tuberosities are less strongly developed and the greater palatine foramina are not found posterior to M^3, even in *P. major*. There appears to be no correlation with sex in these features, and indeed

one of the specimens with alveolar tuberosities most strongly developed is a probable female of *D. macinnesi* (KNM-RU 1774).

All hominoids preserve the primitive primate heritage of maxillary and sphenoidal sinuses (Cave & Haines 1940). This condition is present in hylobatids, but it has been complicated in various ways in pongids. In the orang-utan the maxillary sinus has expanded at the expense of the sphenoidal sinus, occupying an enormous area in the maxilla and the sphenoid, and extending posteriorly into the pterygoid and palatine processes and temporal bone and superiorly into the frontal bone. No explanation is given by Cave & Haines (1940) for this extensive pneumatization but it is interesting, for the orang-utan has the least robust skull of the living pongids. The chimpanzee and gorilla share with man the development of the ethmoidal sinus, an offshoot of which is the twin frontal sinus (Cave 1961). They also have extensive maxillary and sphenoidal sinuses, the former penetrating down between the roots of the molars so that the floor of the sinus is divided up into many loculi.

Of the Kenya Miocene apes, *P.* (*R.*) *gordoni* has conspicuously the most extensive maxillary sinus, as judged by the area of the floor of the sinus. It is followed closely by *P.* (*R.*) *vancouveringi* (Table 23, no. 2). The floor of the sinus penetrates deeply between the roots of the molars, although no separate loculi are formed, and it extends laterally into the zygomatic processes of the maxilla. By contrast the species of *P.* (*Proconsul*) appear to have more restricted maxillary sinuses, especially *P. africanus*. *Dendropithecus macinnesi* has a fairly extensive maxillary sinus, the floor penetrating between the molar roots nearly as deeply as in *P.* (*R.*) *gordoni*, but it does not extend as far laterally as in the latter species. A fronto-ethmoidal sinus like that of the African apes and man is known in *P. major* (Pilbeam 1969). The apparent parallelism of maxillary sinus development between *P.* (*R.*) *gordoni* and the modern apes, particularly the orang-utan, is interesting, but it is probably of little taxonomic significance. Similarly with the relatively small maxillary sinus of *P.* (*Proconsul*); but the presence of a true frontal sinus in *P. major* is probably significant in that the true frontal sinus (cf. Cave 1961) is only known in *Pan* and in hominids, and is absent in the orang-utan and gibbon and all other primates.

Palatal shape in modern pongids is very distinctive. The intercanine distance is as great as or greater than the intermolar distances so that the palate has a rectangular appearance. In hylobatids, and most of the fossil apes, the palate is narrower anteriorly, only *P. major* differing from these and resembling the modern apes (Table 23, nos 3–4).

Mandible. The mandibular symphysis in pongids has been the subject of much controversy. Symphyseal cross-sections have been discussed in great detail by Goodman (1968), but so great is the variability in morphology that it is not possible to distinguish absolutely between the three living pongid species. All are alike in having an inferior transverse torus, which stretches posteriorly as far as P_4/M_1 in the orang-utan and to M_1 in the gorilla and sometimes in the chimpanzee (Goodman 1968). (I distinguish here between the inferior transverse torus, which is some way removed from the inferior edge of the symphysis and which has the digastric impressions on its inferior surface, and the simian shelf which is an infolding of the inferior edge of the mandible at the symphysis and which has the digastric impressions medially or even slightly superiorly.) The development of an inferior shelf (simian shelf) is much less common in the gorilla than in the chimpanzee and orang-utan. Correlated with this is the shallower and constricted genial fossa in the gorilla compared with the deeply indented fossa in the other two.

The symphysis of most of the dryopithecines differs strikingly from that of the modern apes. None of these Miocene pongids has anything approaching a simian shelf, although the inferior transverse torus may be developed in some Eurasian species, for example *S. indicus* and *D. fontani*. In the African species the superior transverse torus is always well developed and is relatively larger on the larger species, reaching its maximum development in *P.* (*R.*) *gordoni* and *P. major*. The Miocene pongids had more robust symphyses than modern pongids (Table 23, no. 5), but despite these differences all the Miocene pongids fall on the same log regression line (symphysis thickness plotted against mandibular tooth row length $C–M_3$) with the modern pongids, indicating that the same allometric relation holds throughout. *Dendropithecus macinnesi* differs from the dryopithecines, but resembles the Oligocene *Aegyptopithecus zeuxis*, in having an inferior torus that often projects posteriorly further than the superior torus. The development

of the inferior torus varies greatly, but it is as distinctive a feature as it is in modern apes. It is particularly well developed on the Songhor specimens of *D. macinnesi*.

The body of the mandible in modern pongids shows very great variation in size between males and females. It gets shallower posteriorly in both pongids and hylobatids, but more so in the latter. The degree of robusticity is much less in the hylobatids, and in the pongids it is least in the orang-utan which tends to have a relatively deep gracile mandible. The divergence of the tooth rows is greatest in the gorilla mainly because the breadth across the canines is less in this species than in the other pongids. Both chimpanzee and orang-utan have rather broad parallel tooth rows. The degree of robustness of the mandibular body of the Miocene pongids follows closely that of the symphysis (Table 23, no. 6). The variation in size is at least as great as in modern pongids of equivalent size, and often greater. Like the symphysis the body of the mandible in Miocene pongids is often more robust than in modern apes. The mandibular tooth rows diverge more strongly in the fossil apes, although the modern pongid condition is approached by *P. major* (Table 23, no. 8).

Incisors. Compared with other groups of mammals, hominoid primates have relatively large incisors. The central incisors are broad and spatulate, and the upper ones often have a central pillar or tubercle. The lateral incisors are asymmetrical, but while the uppers are often more or less pointed, the lowers always retain a flat incisive edge continuous with that of the central incisors. Chimpanzees and orang-utans have relatively larger incisors than other pongids.

The dryopithecines have relatively small incisors compared with modern pongids. *P. major* and the two Indian species of *Sivapithecus* have the largest I^1s relative to M^1 size (Table 23, no. 30). The other species all have smaller incisors relative to M1, but they are of approximately the same relative breadth as those of modern pongids (Table 23, no. 9) and in some cases are broader, e.g. the species of *P.* (*Proconsul*). It would appear, therefore, that it is in the buccolingual dimensions that the fossil pongid incisors are smaller than those of modern pongids, or in other words that the incisors were less stout. This is emphasized by the fact that the crown heights are relatively higher in the fossil pongid incisors, especially in *P.* (*R.*) *gordoni* and the Asian *Sivapithecus sivalensis*, than in the modern pongids (Table 23, no. 10). In addition, there is a greater size difference between I^1 and I^2 in *P.* (*Proconsul*) than in other dryopithecines or in modern pongids, the I^1 being spatulate and the I^2 more of a narrow blade (Table 23, nos 11 and 12). This is not the case in *P.* (*R.*) *gordoni*. The Miocene hylobatids, *Dendropithecus macinnesi* and *Pliopithecus* species, are similar to modern hylobatids in most of these features, but differ in the incisors being higher-crowned. As a whole the hylobatids have smaller incisors relative to M1, relatively narrower and higher crowns, and less spatulate I^1s compared with pongids. These features are also shared by the isolated incisors attributed to *Aegyptopithecus zeuxis*. Nearly all of the incisor samples of Miocene apes are small and little can be said about variability. The bivariate plots (Figs 9–10 and 17–18) show the size variation which is of the same order as that of equivalent-sized modern apes. Morphological variation is less than that of modern apes, probably as a result of lack of representation in the smaller samples.

Canines. The canines are variable in size but are always pointed tusk-like teeth in modern pongids. The crown of the upper canine is bilaterally flattened, although this is not necessarily reflected in the dimensions at the base of the crown. The long axis of the tooth is in line with or only slightly divergent from the line of the premolar series. The lower canine is more oblique. It is also more asymmetrical since the mesial ridge is well developed and the distal ridge is not; the upper canines have both mesial and distal ridges well developed and continuous over the apex of the tooth. The upper canines are worn both mesially and distally, the former by occlusion with the lower canine, producing a flat wear facet, and the latter by occlusion with the P_3, producing a concave wear facet cutting across the distal ridge. In living pongids this grinding action of the flat surface of the P_3 against and into the concave facet of the upper canine cannot be described as sectorial because it blunts rather than sharpens the canine. The wear on both the C and the P_3 starts at the tip and in some individuals never passes along the crown, so that both teeth are worn flat. This condition has been referred to by Wolpoff (1971). More usually, however, wear facets are formed along the edges of the crown.

In hylobatids the distal wear facet is distolingual. The anterobuccal face of the P_3 occludes against the lingual edge of the distal ridge of the upper canine, so that attrition has the effect of sharpening the canine tip and the edge of the distal ridge. This means that throughout the effective life of the tooth the upper canine is maintained with a sharp distal cutting edge. This condition has been described for the Cercopithecoidea (Zingeser 1969; Every 1970), in which the P_3 acts as a grindstone to sharpen the point and distal edge of the upper C, as canine honing, by which the unworn pointed tip of the canine is maintained by wear.

The canines in dryopithecines tend to be less tusk-like and less robust than in modern pongids, but this is a qualitative assessment and is not reflected in any of the indices. This arises because the indices are based (necessarily) on the dimensions of the base of the crown (Table 23, no. 13), and these are quite similar between fossil and modern pongids. The crown above the base tapers more in the fossil canines, and this makes them appear less robust, but it has not been found possible to illustrate this by any repeatable measurement or index. The fossil hylobatids differ strongly from the modern ones in having lower-crowned canines and in displaying a higher degree of sexual dimorphism. They are similar in having the truly sectorial C–P_3 complex found among the Hominoidea only in the Hylobatidae; the wear of the P_3 on the upper C of *D. macinnesi* has a sharpening action on the distal edge of the canine. What is known of *Aegyptopithecus zeuxis* suggests that it resembles the hylobatids in canine morphology.

Morphological variations are greater in the fossil apes than those seen in the modern ones. This is particularly true of cingulum development, which may be strongly developed or absent altogether within one species. Mesial groove development in the upper canines is also variable; it is most striking in *D. macinnesi* in which the upper canine in males has two prominent mesial grooves and in females has one shallower groove. The bivariate plots for the canines are shown in Figs 11 and 19. Much larger samples were available than for the incisors, and it is probable that something approaching the full range of variation is present for both canines in *Dendropithecus macinnesi*, *Limnopithecus legetet* and *P. nyanzae*, and for the upper C in *P. africanus* and *P. major*. The lower C ranges for *P. africanus* and *P. major* are obviously too limited, either as a result of sample bias or of incorrect identification of isolated teeth. In either event, more complete material, in which canines are definitely associated with molars, is necessary before the whole picture can emerge.

Lower third premolar. P_3 is usually one-cusped in modern pongids, but a smaller lingual tubercle is often developed on the lingual ridge. The axis of the tooth is set obliquely to the molar tooth row, and the enamel at the anterior end of the long axis (the mesiobuccal angle of the tooth) is extended inferiorly down the mesial root of the tooth. In hylobatids, the tooth is more in line with the molars, but it still has the inferior extension of the enamel on the buccal side of the tooth. Also in hylobatids the lingual ridge is poorly developed. The function of P_3 in hylobatids is completely different from that in pongids, as just discussed in the last section. In pongids the tooth is undergoing molarization in a manner similar to, but much less advanced than, that of hominids, and there is a lot of variation in the extent to which molarization has occurred. Variations occur particularly in the degree of development of the lingual cingulum, and in the breadth/length index, which varies from 60% to 80% in the chimpanzee and gorilla and from 50% to 60% in hylobatids.

In the Miocene pongids the morphology and variability of the P_3 is very similar to that of the modern pongids. Correlated with the blade-like crown of the canines is the probably greater degree of sectoriality in the fossil pongids (Table 23, no. 18). This is particularly marked in *P.* (*R.*) *gordoni* and *P. nyanzae* in which sectoriality in function is correlated with two P_3 indices, the breadth/length index and the mesial extension of enamel index (Table 23, nos 19 and 20). The height of the crown would also appear to be correlated, but in this case in the fossil hylobatids it is very high-crowned (*D. macinnesi* and *Pliopithecus* spp.) while in *Hylobates* itself it is low-crowned (Table 23, no. 21). Unfortunately there is no crown of the P_3 of *Aegyptopithecus zeuxis* yet known. The degree of molarization in the fossil pongids appears to be rather less than in modern ones. A small lingual cusp is sometimes developed, particularly in *L. legetet*, but it is by no means common. Lingual cingula are usual in the fossil P_3s. In the bivariate plot for this tooth (Fig. 20) it can be seen that, so wide are the ranges of variation, there is considerable overlap

between the larger species of *P.* (*Proconsul*). The relatively elongated crown in *P.* (*R.*) *gordoni* is also shown in this figure.

Finally, in the discussion of the P_3, special mention must be made of *P.* (*R.*) *gordoni.* If the specimens known are correctly attributed to this species it differs strongly from the other dryopithecines and from other pongids, but once again the differences are not reflected in the indices, except in the degree of bilateral compression (Table 23, no. 19). The tooth is very big, both in mesiodistal length and in height; the lingual and buccal borders are nearly parallel, and there is no mesial angulation of the anterior end of the crown as seen in most fossil and living pongid species. In this respect the crown resembles those of hylobatids, but whereas in the latter the long axis of the crown is nearly in line with the axis of the molar tooth row, in *P.* (*R.*) *gordoni* the long axis of the P_3 is strongly oblique. The wear facet is nearly perpendicular to the long axis at the anterior end of the crown, which faces anterobuccally so that the distal wear on the upper C must have been lingual rather than distal. As a result the distal edge of the upper C would have been sharpened by the lingual wear rather than blunted by distal wear, i.e. the wear would have been sectorial.

Lower fourth premolar. The P_4 is always bicuspid in modern pongids, the buccal cusp being the larger of the two. The talonid is well developed. The roots are set obliquely in the mandible, paralleling the orientation of the P_3. In hylobatids the crown is longer than broad; in the orangutan it is nearly square; while in the chimpanzee and gorilla the crown is usually broader than long. In the Miocene pongids, the P_4 is so variable that it is hard to generalize on its morphology. The long axis of the tooth is nearly always set obliquely to the molar tooth row, paralleling the long axis of the P_3. Different degrees of obliqueness result in widely different breadth/length ratios if mesiodistal length is used, for the greater the obliqueness the shorter is the mesiodistal length and the wider is the buccolingual breadth. This shows up in the breadth/length ratio (Table 23, no. 22) and can be seen in individual detail in the tables of measurements (Tables 1–21) and in the bivariate plot for this tooth (Fig. 21). The plotted points are particularly widely scattered for *Dendropithecus macinnesi*, *P.* (*R.*) *gordoni* and *P. nyanzae*. As in P_3, there is extensive overlap between the species of *P.* (*Proconsul*).

Upper premolars. In modern pongids the upper premolars are always bicuspid, and the buccal cusp projects further than the lingual one. This difference is more pronounced in the P^3 than the P^4. Also in P^3 the buccal side of the crown is slightly more expanded up the mesiobuccal root in a similar fashion to the P_3. Both upper premolars are three-rooted, the mesiobuccal root being more prominent than the distobuccal one. The P^3 is bigger than the P^4 and is also more variable in size.

In the Miocene pongids the same general pattern emerges with the only variations being in *P.* (*Rangwapithecus*). In this the two upper premolars have a greater degree of molarization: the two cusps are nearly equal in height, the P^3 has no pronounced buccal expansion, the distal cingulum is greatly expanded, and P^4 is larger than P^3 (Fig. 25). In addition, the breadth/length index is lower as a result of the large distal cingulum and despite the presence of a well-developed lingual cingulum on both premolars. These differences are all illustrated in Table 23, nos 24–28. The fossil hylobatids have relatively small upper premolars with strongly projecting buccal cusps, especially on P^3. The breadth/length ratios are very high as well, seemingly independent of lingual cingulum development. The P^3 is approximately the same size as P^4. The main feature shared with modern hylobatids is the projecting buccal cusp on P^3, which is correlated with the sectorial development of upper C and P_3 (Figs 12–13).

Upper molars. Upper molars of pongids and hylobatids are usually broader than long. They are four-cusped with a well-developed hypocone in addition to the three trigon cusps. Supernumerary cusps are uncommon, the so-called carabelli cusp being the most frequent. Variations in the ridge development and the projection of the cusps is similar to that described for lower molars. Wear is usually much heavier lingually than buccally, matching the buccal wear of the lower molars, but it rarely reaches the same extent as in lower molars where the whole buccal side may be worn away down to the roots.

There is more variation in the relative sizes of the upper molars than there is in the lowers. In

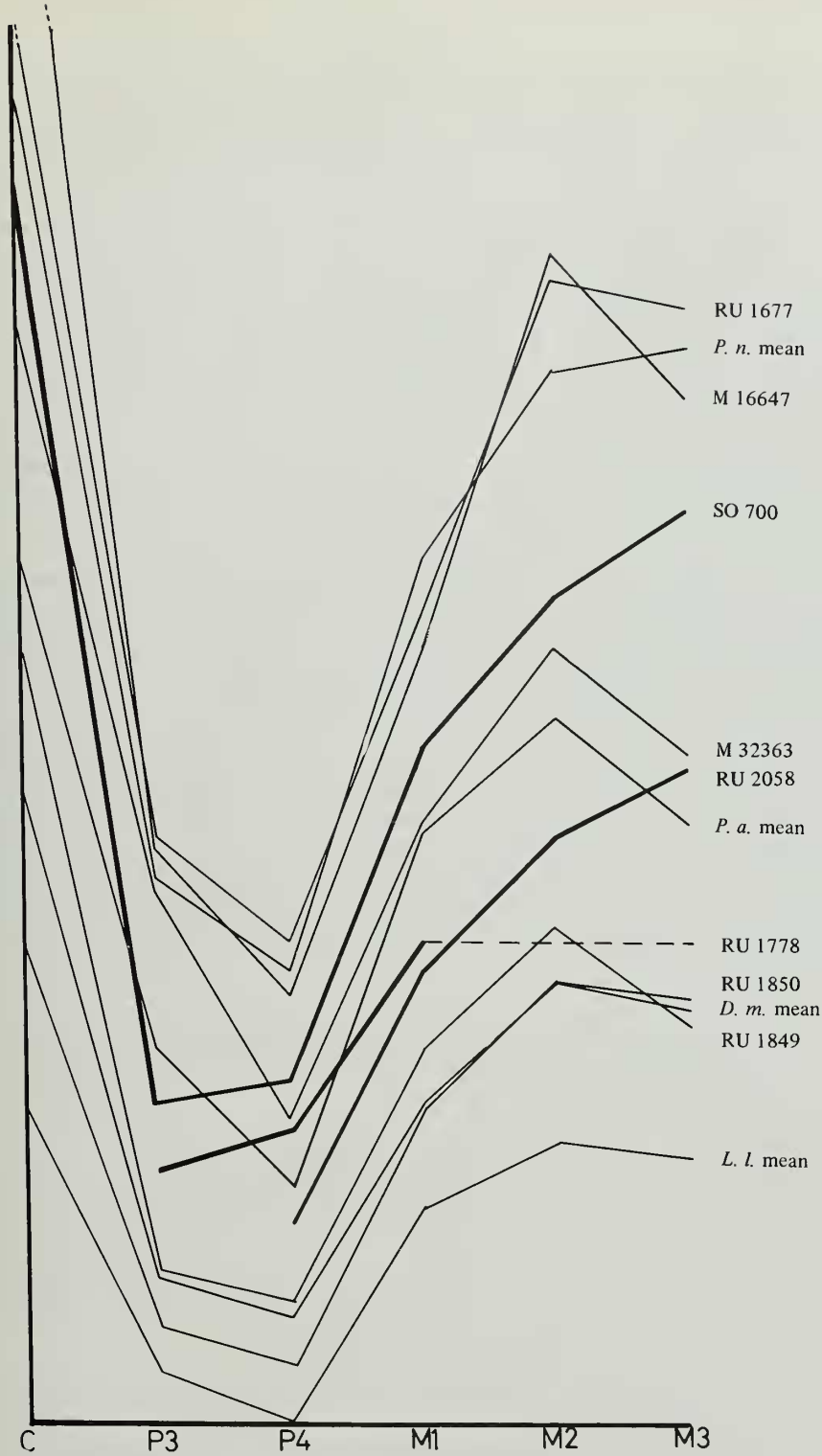


Fig. 25 Relative sizes of C–M³ in Miocene apes, crown module. '*P. n.* mean' is the mean value for *Proconsul nyanzae* with two individual series, M 16647 and RU 1677; SO 700 represents the type specimen of *P.* (*R.*) *gordoni* and RU 2058 of *P.* (*R.*) *vancouveringi*; '*P. a.* mean' is the mean value for *P. africanus* with one individual value M 32363; '*D. m.* mean' is the mean value for *Dendropithecus macinnesi* with two individual values RU 1849 and 1850; '*L. l.* mean' is the mean value for *Limnopithecus legetet*.

the chimpanzees the M^1 is usually the longest tooth, although not always the biggest, because in buccolingual breadth M^2 usually exceeds M^1. M^3 is nearly always reduced. In the gorilla M^2 is usually bigger than M^1, and M^3 is often the longest tooth but is relatively narrower. This variability in relative sizes of the upper molars is a function of variability in the posterior molars, the values for coefficient of variation increasing from M^1 to M^3. In hylobatids the M^3 is usually smaller than M^2, but marginally bigger than M^1. The M^3 is nearly always reduced relative to M^2 in the dryopithecines (Fig. 25). The species follow a consistent pattern, although the degree of reduction of M^3 does vary considerably. Unlike the modern apes, where the M^3 is often smaller than M^1, the dryopithecines have M^3 almost invariably larger than M^1, but smaller than M^2. This pattern is shown in Fig. 25 and in Table 23, no. 33. *L. legetet* and *P. africanus* have the most greatly reduced M3s and *P. nyanzae* the least, while both species of *P.* (*Rangwapithecus*) have greatly enlarged M^3s which are by far the biggest of the upper molars. The contrast between the two subgenera is seen in Fig. 25.

The three trigon cusps of M^1–M^2 tend to be of equal size in the species of *P.* (*Proconsul*). In *P.* (*Rangwapithecus*) the protocone is larger than the others. Perhaps linked with this, the protoconule is developed in the former subgenus but absent in the latter. The ridges connecting the cusps are similar to the modern ape pattern in all species, and it is only the protoconule and cingulum development that distinguishes the upper molars of the fossils.

Another noticeable feature of the upper molars of *P.* (*Rangwapithecus*) is in the breadth/length index (Table 23, nos 29 and 32). In nearly all cases the upper molars are longer than broad, in striking contrast to other dryopithecines in which they are broader than long. There is a very slight increase in the breadth/length index from M^1 to M^3, but nothing like as big as the increases in other dryopithecines and modern pongids. This difference in shape sets them apart from other dryopithecines in the bivariate plots (Figs 14–16). Particularly in Fig. 14 the two species of *P.* (*Rangwapithecus*) can be seen to form discrete clusters below the other dryopithecine samples.

The development of the lingual cingulum in the modern pongids is moderately variable. It is relatively most strongly developed in the concolor gibbon. Of the pongids it is most consistently developed in the gorilla, mostly on the protocone but also on the hypocone. In the chimpanzee the cingulum is confined to the protocone and is larger on M^2 than on M^1. Although smaller on M^3 it is relatively more extensive, running distally nearly to the hypocone. The orang-utan rarely has any cingulum developed. The upper molars of the African dryopithecines are unique in pongids in consistently having a well-developed lingual cingulum. Even some specimens of *P. nyanzae* and *P. major*, formerly assigned to '*Kenyapithecus africanus*', have a slight lingual cingulum on the M^1.

The hypocone is usually a small cusp set directly on the lingual cingulum. Its origin from the cingulum is often clearly seen. In many cases, however, the hypocone itself has a small lingual cingulum encircling it and connecting with the distal cingulum. This is particularly evident in *P. nyanzae*, *P.* (*R.*) *gordoni* and *P.* (*R.*) *vancouveringi*. The last two species also have a very large distal cingulum, and this may be connected with the expansion of the lingual cingulum. The Miocene hylobatids, like the African dryopithecines, have massive lingual cingula on their upper molars. The hypocone is less obviously a cingular structure, although this is not to say that it is not, and there is often a prominent lingual cingulum running around the edge of the hypocone. The M^3 is slightly larger than M^1 but very much smaller than M^2, but the distal cusps are nearly always reduced in size. The molars are relatively broad. In none of these features is there any marked resemblance to modern gibbons, unlike the case of the lower molars. The strong ridge development, the relatively large size of the trigon and the relative breadth of the molars distinguishes these teeth from the contemporary dryopithecines.

Lower molars. Lower molars in modern pongids and hylobatids are almost invariably longer than broad. They have a general pattern of five cusps. Supernumerary cusps are infrequent, occurring most often in the gorilla in the form of an additional buccal cusp(s) next to the hypoconulid. The projection of the cusps above the foveae is greatest in the gorilla and (relatively) in all hylobatids, and is least in the orang-utan. The occlusal ridges are poorly developed, compared with in the Miocene pongids, and are most distinct in the chimpanzee, especially the pygmy chimpanzee, in which both mesial and distal foveae may be sharply delineated. Gorilla lower

molars have a characteristic invagination of the buccal border of the crown which isolates all three of the buccal cusps (the hypoconulid being buccal in most cases) and cuts into and reduces the size of the talonid basin. This condition seems to be fairly standard in gorilla lower molars and contrasts with that of chimpanzees and orang-utans where the talonid basin is relatively wider and the buccal edge of the talonid is less cut into. The latter two species often have some degree of occlusal wrinkling, which is greatest in orang-utans.

In the Miocene pongids the lower molars are basically similar to the modern ones. All the Kenya fossil pongids have a strong buccal cingulum, in contrast to both the Eurasian fossil pongids and the modern pongids. Supernumerary cusps are extremely rare, occurring only on M_3 of *P. major*. The occlusal ridges are well developed, although less so than in the hylobatids, and are distinct on *P.* (*R.*) *gordoni* even though this species has a high degree of secondary wrinkling of the occlusal surface. *P. africanus* has a slight amount of occlusal wrinkling, and it is probable that when the lower molars of *P.* (*R.*) *vancouveringi* become known they will be seen to have wrinkling, but the other species lack it altogether. Another distinctive feature of *P.* (*R.*) *gordoni* is the deep invaginations of the buccal border of the lower molars, which makes them very similar in appearance to gorilla lower molars. *Dendropithecus macinnesi* has relatively elongated lower molars, differing in this respect from *Hylobates*. The general cusp patterns are similar, as are the relative dimensions of the trigonid and talonid basins, but both *D. macinnesi* and *Pliopithecus* spp. have very distinct occlusal ridges that distinguish them both from the dryopithecines and the modern hylobatids. The M_3 is still the largest molar, and not as reduced as in *Hylobates*, but it is smaller relative to M_1 than in the dryopithecines (Table 23, no. 35).

Breadth/length indices of modern pongids are not very variable. All the species of pongid have similar ratios, the one for M_2 being greatest and the one for M_3 least. One difference is the increase in index from M_1 to M_3 in chimpanzees, indicating less elongation or narrowing of teeth. Hylobatids have lower values than pongids (see Table 23). Some vestiges of buccal cingulum on the lower molars are fairly frequent in modern pongids. It is most strongly developed in the gorilla, in which it may run the length of the buccal border of the molar crown, divided into three by the buccal grooves running between the cusps. In chimpanzees, a buccal cingulum is less common and, where present, is confined to the protoconid. In orang-utans the cingulum is reportedly only rarely developed (Frisch 1965). Hylobatid lower molars in general do not have buccal cingula except in *Hylobates concolor* where it may be frequent.

The lower molars in the African dryopithecines are relatively much more elongated than in modern pongids (Table 23, no. 34). This is despite the fact that they have the strong buccal cingulum. In fact there seems to be an inverse correlation between cingulum development and relative breadth of the crown, for the Eurasian dryopithecines, in which the cingulum is poorly developed, are relatively broader than African ones, and the modern pongids, which only rarely have a small cingulum, are broader still. It is possible that the buccal cingulum in *P.* (*Proconsul*) and *P.* (*Rangwapithecus*) may not be a primitive retention, as has been suggested (Clark & Leakey 1951), but may be a progressive feature by which the crown widths, and therefore the total occlusal area, are being expanded. Frisch (1965) claims evidence for a trend in pongids towards reduction and loss of molar cingula. This would apparently be true as a general trend from the Miocene to the present, but before that the trend was going the other way. From *Oligopithecus* to *Aegyptopithecus* to *Proconsul* the molar cingula increased in size, and there is no evidence when this tendency to increase was reversed. If the cingulum is adaptive in increasing molar area, then it seems reasonable to suppose that it would start to be reduced only when the molar occlusal area had increased either at the expense of or incorporating the original cingulum.

The relative sizes of M_3 with respect to M_1 are shown in Table 23, no. 35. In modern pongids, the most common size relationship between the lower molars is an increase in size from M_1 to M_3, but there are several variations on this: in both chimpanzee and orang-utan the M_2 is often the largest, and sometimes even the M_1 (Schuman & Brace 1954); in gibbons the M_2 is often the largest. Frisch (1965: table XV) shows that in terms of mesiodistal length the M_3 is usually shorter than M_1 in all species of gibbon, but since the buccolingual breadth is usually greater the overall size is the same or greater. Molar size increases from M_1 to M_3 in all the African dryopithecines to a greater extent than in modern pongids or Eurasian dryopithecines (Table 23, no. 35; Figs

Table 23 Comparative morphology of fossil and modern apes.

		Dendropithecus macinnesi	*Proconsul (Rangwapithecus) vancouveringi*	*Proconsul (Rangwapithecus) gordoni*	*Limnopithecus legetet*	*Proconsul africanus*	*Proconsul nyanzae*	*Proconsul major*
Maxilla								
index naso-alv. ht/M^2–M^3	(1)	24	–	35	–	42	–	46
maxillary sinus floor	(2)	extensive	extensive	v. extensive	small	v. small	small	small
index pal B at M^2/L × 100	(3)	44	–	41	–	52	49	43
B at C/B at M^2	(4)	97	–	97	–	81	96	109
Symphysis								
robusticity	(5)	moderate	–	gracile/robust	moderate	moderate	moderate	v. robust
index t/d × 100		46	–	56	43	45	47	56
Mandibular body at M_3								
robusticity	(6)	moderate	–	gracile/robust	gracile	robust	moderate	robust
index t/d × 100		50	–	56	48	57	53	55
index M_3d/symph. d × 100	(7)	78	–	77	83	78	75	75
Mandibular breadth								
ant. breadth of mand.	(8)	prob. narrow	–	narrow	narrow	narrow	narrow	broad
index C–C/M_3–M_3		–	–	–	51	47	52	62
Incisors								
length of crown (md)	(9)	v. narrow	–	mod. narrow	broad	broad	broad	broad
I^1 index bl/md × 100		86	–	74	78	75	76	79
I_1 index bl/md × 100		137	–	101	119	126	115	125
height of crown (buc)	(10)	v. high	–	mod. high	moderate	moderate	moderate	moderate
I^1 iodex md/ht × 100		73	–	78	90	90	85	87
I_1 index md/ht × 100		53	–	51	60	43	55	46
shape of I^1	(11)	narrow blade	–	narrow spatulate	spatulate	spatulate	spatulate	spatulate
index I^1md/I^2md × 100	(12)	131	–	122	139	151	151	136
Canines								
bilateral compression	(13)	v. great	–	moderate	little	little	little	little
C^1 index b/l × 100		72	–	71	79	78	80	82
C_1 index b/l × 100		65	–	70	70	72	75	70
height of crown (buc)	(14)	mod. high	–	v. low	moderate	moderate	moderate	moderate
C^1 index l/ht × 100		70	–	99	73	81	76	77
C^1 mesial groove	(15)	double prominent	–	one v. prominent	one shallow	one shallow	one shallow	one shallow
C_1 mesial ridge	(16)	short	–	long	v. short	short	long	v. long
index mes. ridge/ht × 100		69	–	82	61	73	81	92
C_1/M_1 (area) min ♀	(17)	95	–	132	75	85	124	119
max ♂		123	–		115	124	183	153
Lower P3								
sectoriality	(18)	sectorial	–	sectorial	not	not	moderate	not
bilateral compression	(19)	v. great	–	v. great	little	little	moderate	great
index b/t × 100		60	–	58	65	65	63	61
ext enamel mes root	(20)	great	–	moderate	little	little	great	little
index dist. ht/mes. ht × 100		72	–	82	77	76	70	78
height of crown (mes. buc)	(21)	v. high	–	low	low	low	low	low
index l/ht × 100		87	–	111	104	101	105	101
Lower P4								
mesiodistal length	(22)	elongated	–	elongated	elongated	broad	broad	broad
index bl/md × 100		91	–	92	84	108	104	110
buccal cingulum	(23)	weak	–	weak	weak	weak	weak	weak
Upper P3								
buccolingual breadth	(24)	v. broad	narrow	moderate	moderate	broad	broad	broad
index bl/md × 100		168	127	143	148	163	163	149
buccal cusp projection	(25)	v. great	little	moderate	moderate	great	great	great
index buc. ht/ling. ht × 100		170	108	134	141	163	157	161
lingual cingulum	(26)	none	strong	strong	none	none	none	none
Upper P4								
size rel. to P^3	(27)	same	larger	larger	smaller	smaller	smaller	smaller
lingual cingulum	(28)	strong	v. strong	v. strong	strong	none	moderate	weak
Upper M1								
buccolingual breadth	(29)	broad	v. narrow	v. narrow	moderate	moderate	moderate	moderate
index bl/md × 100		127	97	98	121	118	115	116
I^1/M^1 × 100 (module)	(30)	71	–	78	78	79	77	83
lingual cingulum	(31)	v. strong	v. strong	v. strong	strong	strong	strong	strong
Upper M3								
buccolingual breadth	(32)	broad	v. narrow	v. narrow	broad	broad	broad	broad
index bl/md × 100		122	99	99	124	129	119	121
size rel. to M^1 (module)	(33)	sl. larger	much larger	much larger	sl. larger	larger	much larger	larger
index M^3/M^1 (module)		105	118	127	103	110	122	112
Lower M3								
mesiodistal length	(34)	moderate	–	elongated	moderate	moderate	moderate	moderate
index bl/md × 100		80	–	73	82	79	81	78
size rel. to M_1 (module)	(35)	sl. larger	–	much larger	sl. larger	larger	larger	much larger
index M_3/M_1 × 100		124	–	140	118	130	137	158
buccal cingulum	(36)	weak	–	strong	strong	strong	strong	strong

Aegyptopithecus zeuxis	*Pliopithecus* spp.	*Dryopithecus fontoni*	*Sivapithecus sivalensis*	*Sivapithecus indicus*	*Hylobates* spp.	*Pan troglodytes pontiscus*	*Pan troglodytes troglodytes*	*Pan gorilla*	
36	40	–	–	–	48	–	95	66	(1)
–	–	–	small	small	moderate	extensive	extensive	extensive	(2)
37	36	–	–	–	44	–	60	52	(3)
73	77	–	–	–	92	–	118	117	(4)
gracile	moderate	robust	moderate	moderate	gracile	gracile	gracile	moderate	(5)
37	41	50	43	40	35	42	38	43	
gracile	moderate	gracile	robust	robust	gracile	gracile	moderate	moderate	(6)
46	53	49	59	58	49	47	53	53	
75	75	77	74	74	62	88	65	51	(7)
v. narrow	v. narrow	–	–	–	broad	broad	v. broad	broad	(8)
36	43	–	–	–	63	67	75	65	
prob. narrow	v. narrow	–	broad	broad	broad	v. broad	v. broad	broad	(9)
–	97	–	78	77	79	77	80	80	
–	126	–	–	–	106	95	109	117	
high	low	–	mod. high	moderate	v. low	v. low	v. low	v. low	(10)
(74)	89	–	77	89	98	102	103	105	
(57)	50	–	–	–	73	81	74	72	
uncertain	narrow blade	–	v. spatulate	spatulate	narrow spatulate	spatulate	spatulate	spatulate	(11)
–	139	–	128	–	138	138	130	139	(12)
great	moderate	moderate	moderate	moderate	moderate	little	little	little	(13)
74	79	–	78	72	72	79	77	76	
69	68	70	79	78	74	76	80	82	
v. high	v. high	v. high (C_1)	moderate	moderate	ext. high	moderate	moderate	moderate	(14)
68	68	–	82	75	40	78	73	76	
one prominent	one prominent	–	one v. prominent	one prominent	one prominent	one shallow	one shallow	one shallow	(15)
(long ?)	short	moderate	–	moderate	moderate	moderate	long	long	(16)
(79)	66	74	–	76	78	68	80	76	
–	87		108	90	66	97	75	(17)	
–	101	101	95	116	114	86	147	132	
prob. sectorial	sectorial	moderate	not	not	sectorial	not	not	not	(18)
great	little	moderate	moderate	great	great	little	little	little	(19)
62	68	64	64	60	61	71	70	69	
–	moderate	great	little	little	great	v. little	little	little	(20)
–	75	70	83	78	70	91	83	82	
–	v. high	low	low	low	low	low	v. low	low	(21)
–	86	105	115	110	114	102	128	115	
broad	sl. elongated	broad	broad	broad	elongated	broad	broad	broad	(22)
105	98	102	113	122	84	104	115	116	
–	weak	none	none	none	none	none	none	none	(23)
v. broad	broad	–	narrow	narrow	v. narrow	narrow	mod. narrow	mod. narrow	(24)
175	164	–	127	122	104	125	131	133	
great	great	–	great	great	v. great	moderate	great	great	(25)
153	150	–	159	189	214	130	150	153	
none	none	–	none	none	none	none	none	none	(26)
smaller	smaller	–	smaller	smaller	smaller	smaller	smaller	smaller	(27)
strong	strong	–	none	none	none	none	none	none	(28)
v. broad	broad	moderate	moderate	moderate	moderate	moderate	moderate	narrow	(29)
137	129	117	114	111	115	111	113	106	
–	69	–	88	86	77	96	96	83	(30)
v. strong	strong	none	none	none	none–weak	none–moderate	none–weak	none	(31)
v. broad	broad	broad	intermediate	narrow	intermediate	intermediate	broad	narrow	(32)
145	127	130	112	108	113	116	120	106	
larger	sl. larger	–	sl. larger	sl. larger	smaller	smaller	smaller	smaller	(33)
113	103	–	103	108	99	93	93	103	
elongated	elongated	short	short	short	short	short	short	short	(34)
77	74	84	85	85	87	94	98	88	
larger	sl. larger	sl. larger	sl. larger	sl. larger	same size	smaller	same size	sl. larger	(35)
131	116	115	123	124	101	93	102	111	
v. strong	weak	weak–moderate	none	none	none–weak	none	none–weak	none–weak	(36)

22–24). The M_3 is an elongated and triangular-shaped tooth very characteristic of the African dryopithecines. The triangular shape must be seen as a reduction in crown area, the distal end of the crown being much abbreviated. Crown elongation is effected by the large heel-like hypoconulid, but the function of this cusp on M_3 is not known, for it does not appear to occlude with any part of the upper dentition. The triangular form is most strongly developed in *P. major* and *P. africanus* and to a lesser extent in *L. legetet* and *P.* (*R.*) *gordoni*. By contrast the M_3 of *P. nyanzae* is rectangular, with the distal end hardly reduced at all.

Wear patterns in modern pongids show great individual variations, but they follow the same general pattern for all living species of pongids and hylobatids. Wear starts at the tips of the buccal cusps and the hypoconulid, exposing dentine at the tips of the cusps. Later, dentine patches are also exposed on the lingual side, by which time the buccal patches are very large and are expanding lingually to meet the lingual ones. Eventually, all the patches unite so that dentine is exposed over the whole crown. The last stage is usually only reached in gorillas, and even well-worn gibbon teeth may have completely separate wear patches on the tips of the cusps. Chimpanzees are intermediate. Orang-utans, having nearly flat occlusal surfaces to begin with, have a less localized pattern of wear so that the rate of change of wear is much slower.

Wear patterns in the African dryopithecines fall into two categories, neither exactly like those of modern pongids. The three species of *P.* (*Proconsul*) and *L. legetet* show few specimens in which wear has exposed large areas of dentine, and the degree of wear is only slightly greater in the M_1 than in the M_3. This pattern is seen most strikingly in *P. africanus*; in *L. legetet* and *P. major*, the smallest and largest species respectively, rather larger areas of dentine are exposed, but not to the same extent as in the Eurasian dryopithecines and modern pongids. The most heavy wear occurs in *P. nyanzae*, and this species also has the steepest wear gradient in the subgenus. The other category of wear is seen in the two species of *P.* (*Rangwapithecus*): in these there appears to be a very steep wear gradient such that there may be extensive areas of dentine exposed on M_1 at a time when M_3 is still almost unworn. This pattern is evident on the type specimens of both *P.* (*R.*) *gordoni* and *P.* (*R.*) *vancouveringi* (KNM-SO 700 and RU 2058).

The shape of the cusps of *Limnopithecus* has been described by Hopwood (1933 : 439) as low, blunt and rounded, and wearing at the tip to expose the dentine. Clark & Leakey (1951 : 68) refer to the cusps as

> . . . rounded conical tubercles. The summits of the tubercles are raised into attentuated points thinly covered by enamel, so that quite early in the wear of the tooth the dentine is exposed here and thus becomes evident as a pattern of small dots on the occlusal surface of the crown. Further, the cusps are somewhat small relatively to the size of the crown as a whole, and are arranged round the margins of a talonid basin which forms rather a broad shallow cup-like excavation in the centre. In these respects (as well as in size), the lower molars have a striking resemblance to those of the small modern gibbons. They differ, however, in that the conical cusps are more individualized, being clearly demarcated from each other by relatively deep intervening sulci. In *Hylobates*, they tend to be united at the periphery of the talonid basin by interconnecting crests. The enamel in *Limnopithecus* is singularly free from secondary foldings.

In most respects this is a good description of *Dendropithecus* [formerly *Limnopithecus*] *macinnesi* except that new material emphasizes what after all was clearly visible on the type specimen, that the conical cusps are united along the periphery of the talonid by well-developed ridges. The description does not fit the other species that Clark & Leakey (1951) included in *Limnopithecus*, *L. legetet*, except that, in common with all other pongids, the tips of the cusps do become worn first and dentine is exposed.

Size variation in fossil and modern apes

The African Miocene pongids fall into three size groups. The *Proconsul* group consists of three species increasing in size from the smallest, *P. africanus*, to the largest, *P. major*. Paralleling this is the *Rangwapithecus* group, the smaller species, *P.* (*R.*) *vancouveringi*, being smaller than *P. africanus* and the other, *P.* (*R.*) *gordoni*, being larger. Finally, *Limnopithecus legetet* is on its own

as by far the smallest species of Miocene pongid. The hylobatid *Dendropithecus macinnesi* is also on its own, approximating in size to *P.* (*R.*) *vancouveringi*.

The absolute variability in size for each species is shown in the bivariate plots presented in the statistical section (Figs 7–24). There is little overlap in species ranges for the mandibular dimensions (Figs 7–8), and in particular *P. africanus* is widely separated from *P. nyanzae*. The incisor ranges are nearly continuous for each species except for the *P. africanus/nyanzae* ranges in the I^1 which are quite distinct (Fig. 9). *P. nyanzae* and *P. major* are difficult to tell apart on incisor size. The small size and relatively greater breadth of the upper incisors of *L. legetet* make this sample distinctive.

The canine ranges are not consistent between uppers and lowers (Figs 11 and 19). In the upper canine the three species of *P.* (*Proconsul*) have relatively large ranges of variation, particularly *P. africanus* which exceeds even *P. major* in this respect, and there is scarcely any overlap between them. In the lower canines, *P. nyanzae* has the largest range and completely overlaps the limited *P. major* range. *L. legetet* also has a much greater range than in the upper C, and *P. africanus* has a smaller range. These vagaries of sample variation are presumably a result of incomplete or biased samples, and where the ranges of variation are so different for two closely allied teeth it would seem reasonable to take the larger of the two ranges as that typical of the species. For instance, the degree of variability for the upper canine of *P. africanus* can be applied to the actual variability of the lower canine to estimate its probable variation, given a more complete sample.

The ranges of variation of the upper premolars (Figs 12–13) have extensive areas of overlap between all species except in P^4 of *Rangwapithecus*. The two species of this subgenus are not very different in size in P^4 dimensions, but both are distinct from the other Miocene species because of their narrow breadth relative to length. The lower premolars also have extensive areas of overlap between the species (Figs 20–21). In the case of P_3 the samples appear to be unusually variable, and this is confirmed by the comparison with modern ape ranges. The chimpanzee range overlaps but is less than that of *P. nyanzae*, and the gorilla range overlaps but is less than that of *P. major*. Since the other fossil species appear no less variable than these two, making due allowance for size decrease, it would seem that the P_3 was more variable in the Miocene than at present.

The ranges of the upper molars (Figs 14–16) show a clear distinction between the species of *P.* (*Rangwapithecus*) and the others. These two species are also quite distinct from each other, even in M^1, and in M^3 their ranges are far apart. *P. nyanzae* overlaps with *P. africanus* in M^1–M^2 but not in M^3, because in the larger species the M^3 is less reduced, widening the gap between them. The M^3 is poorly known for *P. major*, but in the other two molars it appears substantially bigger than in *P. nyanzae* although there is still extensive overlap.

The lower molars have similar patterns to the upper molars (Figs 22–24). There is a slightly greater degree of overlap between *P. africanus* and *P. nyanzae* due to the presence of the two female mandibles of the latter, KNM-RU 1674 and 2087. As has already been seen this overlap is not matched in the mandibular dimensions of these specimens, nor in the C–P_3 dimension, and neither is it in the upper dentition which is associated with RU 1674. Thus although it is tempting to view these two specimens as the wanted male mandibular specimens of *P. africanus*, in most respects they are more similar to *P. nyanzae* (cf. Greenfield 1972).

It can be concluded from this discussion that the ranges of the larger fossil species are comparable with those of the more variable of the modern great apes. In particular, the differences in the ranges of variation of *P. nyanzae* and *P. major* are strikingly like the differences between the chimpanzee and gorilla and this lends support to the validity of these species.

One of the problems in comparing the sample variation in different-sized species is that the species with a larger overall size will have a similarly larger range of variation. The statistic devised to overcome this drawback, the coefficient of variation, has problems of usage itself, especially the lack of precision of the coefficient value. For instance, in small samples of up to ten the standard error of V will be nearly a quarter the value of V and assigning 95% limits will give V a probable range as big as itself. This is an argument against using small samples, but unfortunately small samples are often all that are available in the study of fossils. In this study standard deviations and coefficients of variation have been calculated for samples greater than

ten, and in a few cases for smaller samples, but in many of these the probable (0·95) range of the coefficient of variation is so high as to make it useless. An index that I have devised parallels the effect of the coefficient of variation but, since it takes account of sample size, it allows a probability to be assigned to it; this is arrived at by dividing the range of the 95% confidence limits by the mean rather than the standard deviation by the mean, thus:

$$\frac{t_{0\cdot95}^{N_a} \times 2s_a}{\bar{X}_a}$$

where

N_a = sample size for variable a
s_a = standard deviation of variable a
$\bar{X}_a$ = mean of variable a

The results of using this index are shown in Table 24. The relatively high degree of variability of *D. macinnesi* is emphasized. *P.* (*R.*) *gordoni* is less variable except for the M_3 which is an enlarged tooth in this species. The upper dentition of *P. africanus* is conspicuously more variable than the lower dentition, and this raises the question already commented on, that there do not appear to be any large (male) mandibles of this species in the collection.

An attempt has been made to illustrate this variation in Figs 26–27. These show the mean and 95% confidence limits for dimensions of M^1 and M^3. In certain cases the samples were considered too small to calculate the standard deviation, and in these cases the total range of the sample is shown by dashed lines instead of the 95% confidence limits.

Dendropithecus macinnesi is shown to have high ranges of variation, higher than *Hylobates* and the joint sample of *Pliopithecus*: *P. antiquus* and *P. vindobonensis*. *D. macinnesi* has a lower absolute variation than the chimpanzee, but this is to be expected in a smaller animal, and the M^1 is nearly as variable as in *Papio ursinus* (Freedman 1957).

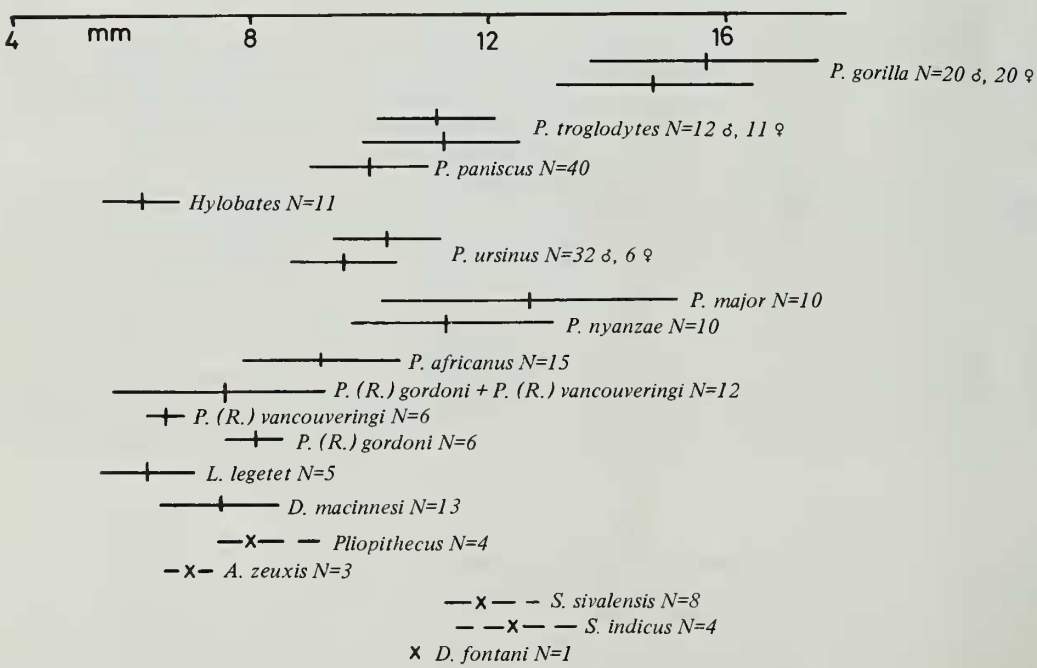


Fig. 26 Variation in M^1 buccolingual breadth (bl): 95% confidence limits.

Table 24 Standardized variation of dental mesiodistal lengths.

md	*D. macinnesi*	*P. (R.) gordoni*	*P. (R.) vancouveringi*	*L. legetet*	*P. africanus*	*P. nyanzae*	*P. major*
$\underline{C}$	61	35	–	38	52	39	30
M^1	24	15	21	20	26	39	45
M^2	32	–	–	22	35	–	–
$\underline{M}^3$	44	–	–	30	36	41	–
$\overline{C}$	53	–	–	47	31	32	–
M_1	24	24	–	21	20	23	30
M_2	21	17	–	22	21	36	–
M_3	38	47	–	32	31	44	–

Limnopithecus legetet is much less variable than *D. macinnesi* and is on a similar level with the comparable-sized *Hylobates*. It is quite distinct from *P. africanus* and *P.* (*R.*) *gordoni* with no points of overlap in range. The latter two species are similar in size, but since they are distinguished entirely by morphological differences this similarity is not significant. More important is the overlap between *P. africanus* and *P. nyanzae*, and between *P. nyanzae* and *P. major*. There are a number of morphological features distinguishing the first pair, but it is difficult to separate the latter two morphologically. However, the range for M^1 of *P. major* exceeds that of the gorilla and that of *P. nyanzae* approximates to that of the chimpanzee (including the pygmy chimpanzee), and a *t*-test on the statistical difference between the samples gives a probability of 0·02 that they represent

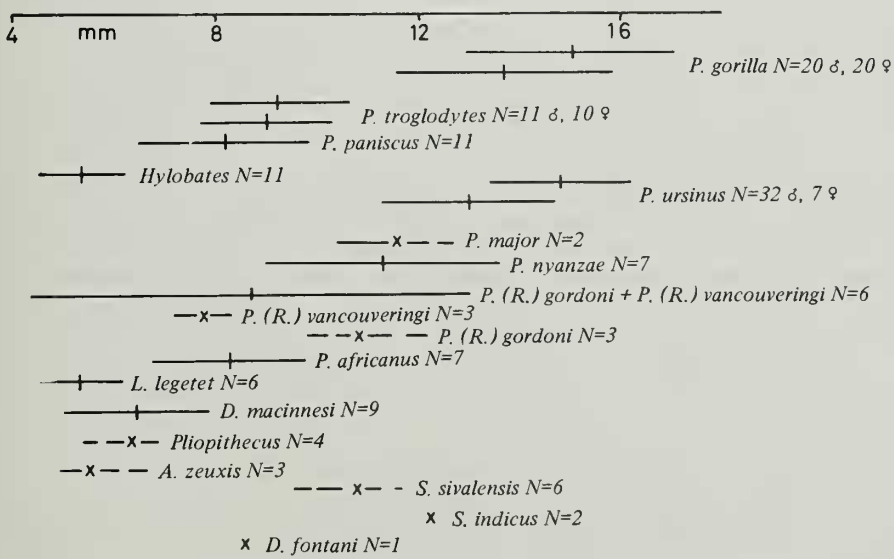


Fig. 27 Variation in M^3 buccolingual breadth (bl): 95% confidence limits.

a single population. On this evidence, therefore, it is unlikely that *P. nyanzae* and *P. major* belong to the same species.

A similar problem was faced with the two *Rangwapithecus* species, *P.* (*R.*) *gordoni* and *P.* (*R.*) *vancouveringi*, although in this case there is no overlap in size ranges. Experimental combined sample ranges of these two species were calculated for Figs 26 and 27. In the case of M^1 this combined range equals that of the chimpanzee and is less than that of the gorilla, both much larger animals, while for M^3 their combined range is nearly twice that of the gorilla. A *t*-test on the differences between the means of the two samples of M^1 gives a probability of much less than 0·001 that they could come from one population. This is strong evidence for some degree of separation between the two groups, and is considered sufficient here to justify specific separation.

A final attempt to quantify the variation in the samples of Miocene apes was by means of multivariate analysis. The results are presented here of an untransformed cos θ analysis (Andrews 1973; Andrews & Williams 1973) based on the incisor and canine dimensions together with those of the symphysis and premaxilla. This method has removed the primary effects of size, but it has failed to distinguish between size-related shape changes (allometric) and structural changes in morphology. Similar analyses of the 'sectorial' dentition (Cs, P_3, P^3, symphysis and anterior mandible and maxilla dimensions) and the posterior dentition (upper and lower P4–M3, posterior mandible and maxilla dimensions) gave similar results, but transformed or unnormalized analyses were so heavily weighted by size differences that they provided no new information.

The removal of size as the dominant influence in the multivariate analysis can be seen in the distribution of individuals in Fig. 28. The basic division seems to be between species with relatively high-crowned canines and small symphyseal areas on the left, particularly the modern hylobatids, and species with lower-crowned but more massive canines, large incisors, and more robust symphyses on the right. This is consistent with morphological evidence, the gibbon having the most exaggeratedly high-crowned canines; this feature is shared, though to a lesser degree, by *Aegyptopithecus*, *Pliopithecus*, and *Dendropithecus macinnesi*. *Limnopithecus legetet* with its large incisors, small canines and small symphseal area is predictably midway between the chimpanzee and *P. africanus*, and these form a group with *P.* (*R.*) *gordoni* at the opposite end of the scale from the hylobatids. The slight divergence of *P. major* and the gorilla and orang-utan may be significant, but it is difficult to be certain on the available evidence.

The multivariate analysis was not as informative as was hoped, but some interesting points have emerged. The analysis of the anterior tooth measurements, as shown in Fig. 28 and four other sets of calculations not shown here, points to a high degree of correlation between canine cross-sectional area, incisor heights, and symphysis cross-sectional area. Canine heights are negatively correlated with these in the multivariate function. Discriminating principally by these factors, the analyses distinguish the hylobatids, with their high-crowned canines and small symphyses, from the pongids with relatively low-crowned canines and large symphyses. Linked with the modern hylobatids are *A. zeuxis*, *Pliopithecus* spp., and *D. macinnesi*; with the modern pongids are linked all the dryopithecines including *L. legetet*.

The analysis of the sectorial tooth measurements points to a positive correlation between upper and lower canine heights. The heights of the main cusp in both upper and lower P3 were negatively correlated with canine heights in the multivariate function but generally positively correlated with P4 size. This is puzzling and indicates that the multivariate function, while discriminating mainly on the degree of sectorial development of the dentition, is not entirely limited to this functional complex. The results show that, while the modern hylobatids have a higher degree of sectoriality than fossil hylobatids, the modern pongids have a lower degree of sectorality than the fossil pongids. It does not seem possible to generalize further than this, and it is unlikely that individuals at the smaller end of the size-range can be compared directly with those at the larger end.

The analysis of the posterior tooth measurements points to a negative correlation between anterior mandibular widths (and symphyseal area) and tooth row lengths. This served to distinguish the modern pongids from all the rest on the basis of their deep symphyses and great anterior widths of the mandible. At the opposite extreme was *A. zeuxis* with its posteriorly-diverging tooth rows.

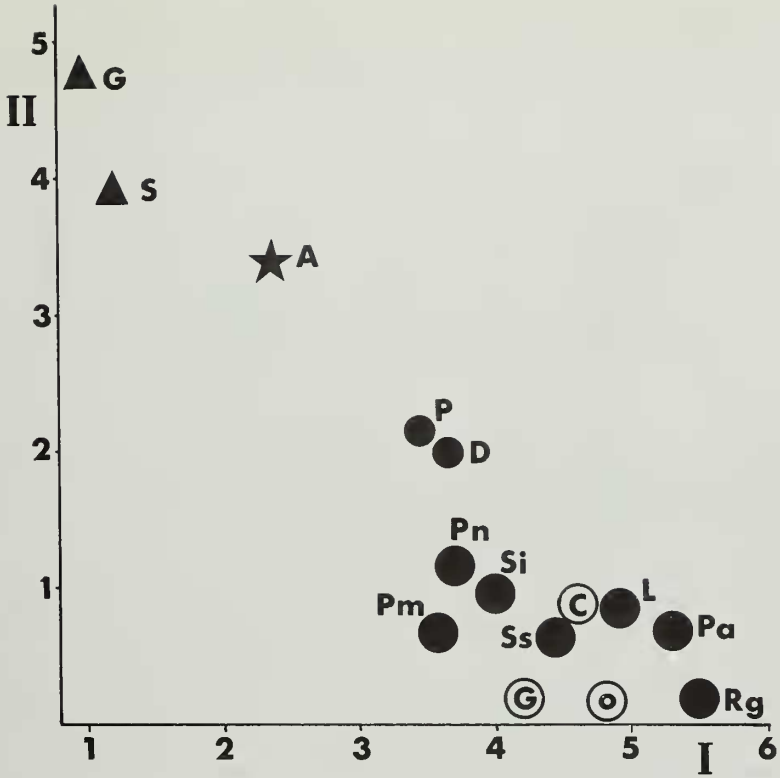


Fig. 28 Principal components analysis of the anterior dentition, principal components I and II. Key: G Gibbon, S Siamang, C Chimpanzee, G Gorilla, O Orang-utan; Pa *Proconsul africanus*, Rg *Proconsul* (*Rangwapithecus*) *gordoni*, Si *Sivapithecus indicus*, Pm *P. major*, Pn *P. nyanzae*, Ss *S. sivalensis*; D *Dendropithecus macinnesi*; L *Limnopithecus legetet*; P *Pliopithecus* species; A *Aegyptopithecus zeuxis*.

Ecology of the African Miocene Hominoidea

It has recently been shown (Andrews 1973, pt. II; Andrews & Van Couvering 1975) that the Miocene apes of Africa probably inhabited forest environments. In the early Miocene the continental divide separating the western equatorial forests from the eastern arid zone was, in the absence of the East African highlands, along the edge of the present eastern rift valley (see Fig. 1). As a result, the western part of East Africa, where most of the Miocene sites are located (see Fig. 1), was probably geographically and climatically part of what is now the Congo basin, so that the equatorial lowland forests, at present limited by the wall of the western rift (Keay 1959), covered most of this region. Forest-adapted land gastropods (Verdcourt 1963) and small mammals in the fossil faunas, and forest trees in the floras (Chesters 1957; Andrews & Van Couvering 1975), correlate with this in suggesting that these sites were sampling forest environments.

A number of fossil ape species have been found in direct association with forest faunas. Association here means at the same level in an excavation, so that probably only one depositional event is represented. (There is no guarantee, of course, that all the bones deposited together come from animals living at the same time in the same place.) *Dendropithecus macinnesi* and *Proconsul africanus* are known from two excavations each on Rusinga Island in association with faunas with strong forest affinities (Clark & Thomas 1951; Whitworth 1953; Verdcourt 1963, 1972; Andrews 1973; Andrews & Van Couvering 1975). Similarly, *Limnopithecus legetet*, *P. major*, and *P.* (*R.*) *gordoni* are each known from two excavations at Songhor in association with similar

Table 25 Distribution of Miocene pongids and hylobatids in Africa (numbers of individuals).

Rusinga	*P. africanus*	*P. nyanzae*	*P. major*	*P. (R.) gordoni*	*P. (R.) vancouveringi*	*L. legetet*	*D. macinnesi*
R1	3	8	–	–	–	1	9
R3	6	3	–	–	–	1	11
Kamugeri	–	–	–	–	–	–	1
Hiwegi general	1	2	–	–	–	–	2
Hiwegi total	10	13	–	–	–	2	23
R100–105	3	1	–	–	–	1	3
R106	6	6	–	–	2	1	4
R107–112	1	4	–	–	–	–	1
Kiahera Hill	–	3	–	–	–	1	1
Kiahera total	10	14	–	–	2	3	9
Kaswanga	13	13	–	–	1	1	12
Sienga	2	–	–	–	–	–	–
Wanyama	–	1	–	–	–	–	–
R114	1	–	–	–	–	–	–
Gumba	1	–	–	–	–	1	–
R2	1	2	–	–	–	1	4
R4	–	1	–	–	–	–	1
Wakondu	–	–	–	–	–	–	1
Kulu total	1	3	–	–	–	1	6
R113 (Kamasengere)	3	3	–	–	–	–	4
R73 (Kalim)	–	1	–	–	–	–	–
Locality unknown	–	3	1	1	–	–	6
Rusinga total	41	51	1	1	3	8	60
Mfwangano	5	3	–	1	1	–	5
Karungu	–	2	–	–	–	–	1
Songhor	5	–	15	17	3	19	12
Koru	3	–	3	–	–	6	2
Losidok	–	–	2	–	–	–	–
Maboko	?	3	–	–	3	2	–
Fort Ternan	2	3	–	–	–	4	–
Ombo	–	–	–	–	–	1	–
Kirimon	–	–	1	–	–	–	–
Moroto	–	–	1	–	–	–	–
Napak	–	–	8	–	–	10	–

faunas. *P.* (*R.*) *vancouveringi* is too little known for any conclusions to be drawn, and the remaining species, *P. nyanzae*, is the only one found in associations suggesting non-forest conditions.

It has previously been pointed out (Andrews 1973; Andrews & Van Couvering 1975) that in the African Miocene the apes may have occupied the ecological niches now fully taken over by the cercopithecoid monkeys. The Miocene apes were in general smaller than those of the present day, the range of estimated sizes being from that of a small *Cercopithecus* monkey, e.g. *C. aethiops*, to about the size of a female gorilla. The study of the limb bones, not yet completed, suggests that the species of *Proconsul* had a more generalized monkey-like arboreal form of locomotion than do the modern apes (Clark & Leakey 1951; Clark 1952; Napier & Davis 1959). At the same time, there is little evidence of the presence of monkeys in the early Miocene environments (Pilbeam & Walker 1968; Simons 1969; Delson 1973), which, being similar in structure to present-day forests, must have provided suitable niches for monkey-like primates. It is logical to assume that the relatively monkey-like dryopithecines occupied part at least of this habitat.

It can be seen that up to five species of dryopithecines can occur in the same deposits (Table 25). Two or three of the species may be very common and the others less so. In addition, the single species of *Dendropithecus* also occurs, making a total of six species for at least two localities: see Table 25. This number of species, while unlike the distribution of modern apes, is very like that of the forest monkey distributions, where there can be three to five species of *Cercopithecus*, one species of the more arboreal *Colobus*, sometimes a species of *Cercocebus*, and one species of the more terrestrial *Papio* all in the same patch of forest (Booth 1956, 1957, 1958; Rahm 1965; Dorst & Dandelot 1970; Kingdon 1971; Preuschoft 1973; Groves, Andrews & Horne 1974; Andrews, Groves & Horne 1975; Morbeck 1975). The proliferation of Miocene ape species, from being unlikely when compared with modern ape distributions, becomes more acceptable if they were ecological equivalents of monkeys.

The comparison of the Miocene apes with the Recent cercopithecines can be carried a stage further. Just as the Recent species of *Cercopithecus*, *Erythrocebus*, *Miopithecus*, *Cercocebus* and *Papio* seem to be representatives of a late Neogene radiation of cercopithecine monkeys, so the Miocene ape populations also seem to be representatives of an earlier Neogene radiation. At least two sets of species were so similar to each other as to make their distinction merely one of size, namely *P. nyanzae*/*major*, and *P.* (*R.*) *gordoni*/*vancouveringi*; the other two dryopithecines, while more distinct, were still very similar to the others and to each other. In addition, *Dendropithecus macinnesi* is divided into two distinct geographical forms. The site differences between these pairs suggests either temporal or geographical speciation, or perhaps a mixture of both (see Table 25).

Phylogeny of the Miocene Hominoidea

The Hominoidea are divided into at least three families, the Pongidae, Hylobatidae, and Hominidae. The taxonomic position of controversial forms such as *Ramapithecus* and *Oreopithecus* are beyond the scope of this paper, and only those species that can with a fair degree of certainty be placed in the Pongidae or Hylobatidae are considered here. The main phylogenetic conclusions are presented in Fig. 29.

Dendropithecus macinnesi is included in the Hylobatidae. Not enough is known to say whether it may have been ancestral to modern gibbons, but there is nothing in its morphology that excludes the possibility. There are even some indications that it may have been near the main line of hylobatid evolution, particularly in the limb bone morphology and in the sectorial function of the canines and third premolars (Andrews 1973; Andrews, Simons & Pilbeam 1977). The latter, however, are probably primitive retentions from the ancestral hominoid stock (Delson & Andrews 1975) and therefore cannot be considered as evidence of phylogenetic relationship, except in so far as the contemporary dryopithecine species, like their descendant pongine species, lack these characters. Similarly, the great degree of similarity between *Dendropithecus macinnesi* and *Aegyptopithecus zeuxis* (see Andrews 1970) is based mainly on retention of presumed primitive hominoid characters in both, notably the deep symphysis and body of the mandible, the high-crowned narrow incisors and canines, the sectorial specialization of P_3, and the buccolingual

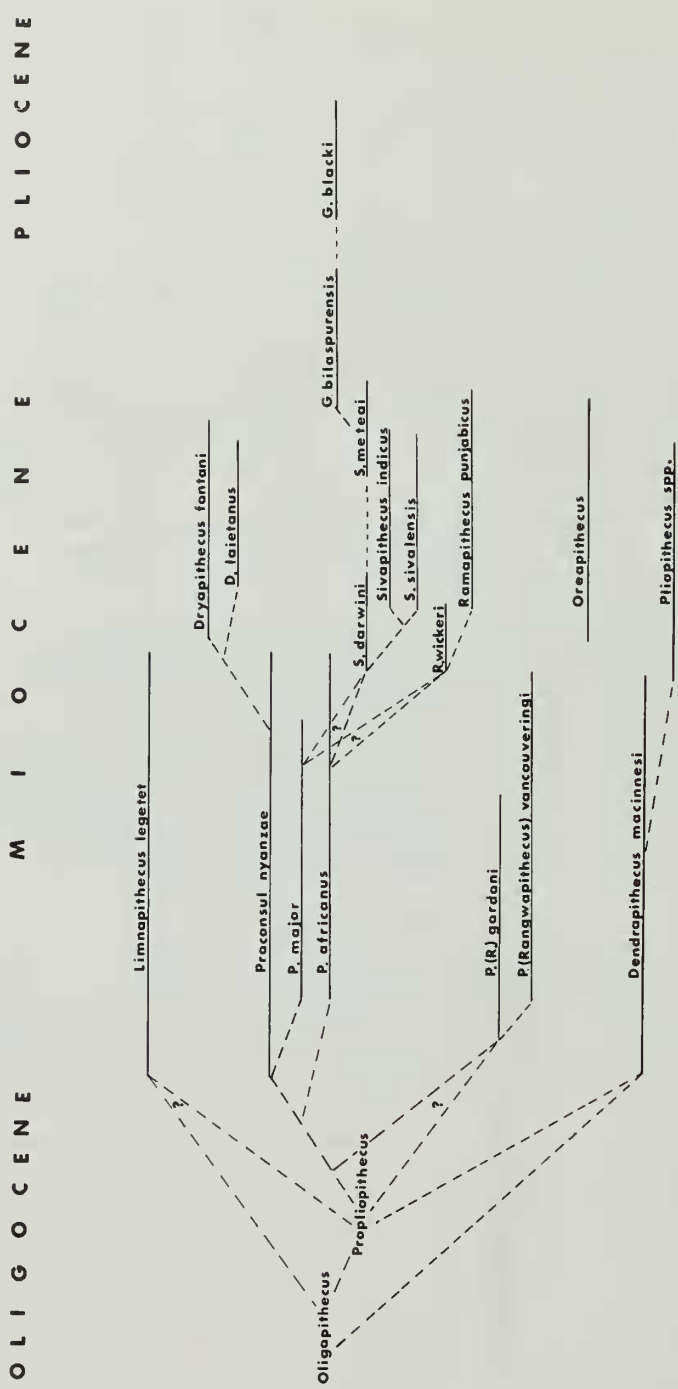


Fig. 29 Phylogeny of the Miocene Hominoidea. Solid lines indicate the life of the species as known at present from the fossil record, and dashed lines indicate possible relationships. If more than one phylogenetic possibility is shown the lines are separated by a '?'. For the purpose of this diagram the Oligocene/Miocene boundary is taken at 23 m.y. and the Miocene-Pliocene boundary at 5 m.y. ago.

expansion and cingulum development of the upper premolars and molars (Delson & Andrews 1975). Since both species have a few presumed derived characters not present in the other, for instance the elongated triangular M_3 and broad ascending ramus in *A. zeuxis*, and the reduced lower molar cingula and large talonid basins of *D. macinnesi*, it makes a direct link between them less plausible.

This matter cannot rest here, however, for there is still dispute over the identification of some of the specimens from the Egyptian Fayum. *Aegyptopithecus zeuxis* was first described by Simons (1965) on the basis of three mandibular specimens. He later added three more mandibular specimens to this species (Simons 1967a : fig. 2; 1971 : fig. 7; Simons & Pilbeam 1972 : pl. 2-1), all from Quarry I of the Fayum (Simons 1967), and a nearly complete skull from Quarry M (Simons 1967). Of these the skull (YPM 23975) and one mandible (CGM 29135) clearly belong with the three specimens of *A. zeuxis* originally described in 1965, but the others, an immature mandible (YPM 23804) and an adult mandible (YPM 23944) are much more similar to the type and only specimen of *Propliopithecus haeckeli* (Schlosser 1911). *P. haeckeli* is very similar to *A. zeuxis*, differing in being slightly smaller and in lacking the specializations of mandible, molar cusp and cingulum morphology, and M_3 enlargement, that characterize *A. zeuxis*. This is the same suite of presumed derived characters that distinguishes between *A. zeuxis* and *D. macinnesi*, and their absence in *P. haeckeli* raises the possibility that it is directly related to *D. macinnesi*. There is, however, too little material of *P. haeckeli* available for such a relationship to be established, and also there is too big a time gap separating the Oligocene from the early Miocene forms.

Propliopithecus is known both from Quarry G and from Quarry I in the Fayum deposits, thought by Simons to be at least 28–30 million years old (Simons 1967). This compares with *D. macinnesi* which is known from the deposits, more than 22 m.y. old, at Karungu (Bishop, Miller & Fitch 1969), and the slightly later deposits at Songhor and Rusinga Island. There is probably thus a time gap of at least 5–6 m.y. between the latest occurrence of *Propliopithecus* and the earliest appearance of *D. macinnesi*, which will need to be filled before it is possible to make any positive statement on the relationships between them.

Simons (1965) suggested that *Aegyptopithecus zeuxis* is similar to later dryopithecines, particularly *P. africanus*. This was based mainly on the lower molar and mandibular morphology. All of the *Aegyptopithecus* specimens known come from the highest levels of the Fayum, Quarry I and M, so that there must again have been a time gap of at least 5 m.y. between these and the earliest known dryopithecine from Kenya.

It has been mentioned earlier that *D. macinnesi* is extremely similar dentally to the European species of *Pliopithecus*. *Pliopithecus* is known in Europe from slightly earlier than 15 m.y. ago to slightly earlier than 12 m.y. After this nothing is known of fossil gibbons until a comparatively recent date, so that on the one hand there is a gap of about 4 m.y. separating *Dendropithecus* and *Pliopithecus*, and about 12 m.y. separating the latter from modern apes. The reason for distinguishing *Dendropithecus* from *Pliopithecus* lies in the post-cranial morphology of the two taxa. In both cases partial skeletons are known associated with cranial and dental remains, and while the limb bones have many points of similarity, those of *D. macinnesi* are more elongated and gibbon-like than those of *Pliopithecus*. This alone is sufficient to suggest that the former was closer to the main line of gibbon evolution than the latter, but there are also some other features of *Pliopithecus* that corroborate this, such as the lack of development of an external auditory meatus, the presence of an entepicondylar foramen on the distal extremity of the humerus (Zapfe 1960), and the absence of laterally placed meniscus markings on the ulnar styloid process (Lewis 1970, 1971). These are primitive features, and their presence does not, therefore, rule out the possibility of *Pliopithecus* being a hylobatid, but it does make it unlikely that it was directly ancestral to any of the living gibbons since in at least one feature the much earlier *Dendropithecus macinnesi* has the derived gibbon morphology in addition to more advanced limb bones.

The relationships of the species of *Proconsul* to the European and Asian species of *Dryopithecus* are still highly conjectural. The earliest dryopithecine known in Eurasia occurs in somewhat later deposits than those of *Pliopithecus*, so that there is a gap in the fossil record of at least 5 m.y. The presence of three of the African early Miocene dryopithecine species at Fort Ternan, more or less contemporary with the occurrence of the earliest Eurasian dryopithecines, does not help

to fill the gap, as the specimens assigned to *Proconsul africanus*, *P. nyanzae* and *Limnopithecus legetet* appear quite typical of the early Miocene forms of these species and show no signs of evolution towards the Eurasian forms.

There is, however, an increasing body of evidence that the Eurasian dryopithecines did evolve from one or other of the African species. *D. fontani* is extremely similar to *P. nyanzae*, particularly in its lower dentition, but differs in having less elaborated upper molars, which lack lingual cingula, and in having an inferior transverse torus of the symphysis as compared with the superior torus of *P. nyanzae*. Similarly, *S. indicus* is similar to *P. major*, but in this case there are some known morphological intermediates. These are found in a recent collection of about 65 isolated teeth made by Professor H. Tobien at Pasalar in Turkey. The teeth, representing the nearly complete dentition of a large dryopithecine, are from early Middle Miocene deposits as old as the oldest *Pliopithecus* specimens from Europe (Andrews & Tobien 1977). They are thus earlier in time than any known specimen of *S. indicus*, and, although they resemble that species, they have a number of differences which must exclude them from it. The lower molars have retained the buccal cingula and narrow trigonid present in *Proconsul*, while the incisors and premolars are intermediate between *Proconsul* and *S. indicus*. The upper molars are entirely typical of the latter species.

Unfortunately the mandibular and maxillary structure of *Sivapithecus darwini* from Pasalar is unknown. The structure of the mandible is particularly important because the early Miocene *Proconsul–Limnopithecus* group has a highly specialized mandibular morphology. The primitive condition in the anthropoid mandibular symphysis appears to have included an inferior torus (Delson & Andrews 1975), as is present in *Aegyptopithecus*, and the presence in *Proconsul* and *Limnopithecus legetet* of a superior torus, with no inferior torus, is therefore a derived or specialized condition. The later Eurasian dryopithecines, however, all have an inferior torus rather than a superior one, and the possibility must be considered that they evolved from an early Miocene form that similarly retained the inferior torus. *Proconsul* and *Limnopithecus* are excluded from this because of their superior torus, and there is no established alternative.

Arising out of the possibility that *Proconsul* may not have been ancestral to later dryopithecines, special mention must be made of '*Sivapithecus africanus*'. This taxon, first described by Clark & Leakey (1951), and reassigned by Simons & Pilbeam (1965) to *Dryopithecus* (*Sivapithecus*) *sivalensis*, is only known from one specimen, and because of this it is included here with *Proconsul nyanzae* on the basis of size. It is difficult to do otherwise considering the fragmentary nature of the specimen (maxilla with P^3–M^1), but it has a number of distinctive characters that would be important if supported by additional material, characters such as the greatly enlarged premolars, the thick enamel and reduction of lingual cingula, and the buttressing of the alveolar process of the maxilla. It could be that '*Sivapithecus africanus*' will prove to be closer to the line of descent of later Miocene dryopithecines than is *Proconsul* when additional material is recovered.

The most recently-occurring dryopithecine species are known from material from Greece and Turkey. These are late Miocene in age and similar to *Sivapithecus indicus* except that they are much larger. '*Ankarapithecus meteai*', first described for a single mandibular specimen (Ozansoy 1955, 1957), is now known from other specimens (Andrews & Tekkaya, in prep.). It was synonymized with *Dryopithecus indicus* by Simons & Pilbeam (1965), but the additional material makes it look quite different, so that it should stand as a valid species, albeit of *Sivapithecus*, not '*Ankarapithecus*'. Very similar to it, but probably not belonging to the same species, is a more recently described specimen from similar-aged deposits in Greece, *Dryopithecus macedoniensis* (de Bonis *et al.* 1974). These new specimens from Greece and Turkey differ from *S. indicus* in a few characters, but the main difference is that they are very much larger, approaching *Gigantopithecus* in size and suggesting a close relationship with the *Gigantopithecus* lineage.

There is too big a time gap between the Miocene and the present to attempt to say anything on possible phyletic relations between the dryopithecines and living pongids. There are a number of features which suggest strongly that the African dryopithecines as a whole were ancestral to the living great apes. For instance, the articulation of the wrist joint with the ulnar styloid process is very characteristic in all living apes, and something like this condition was present in *P. africanus*, more advanced than in modern hylobatids but less so than in the great apes (Lewis 1970, 1972).

It would appear from this that *P. africanus* was a part of the pongid lineage after the hylobatids had already become differentiated, a conclusion entirely consistent with the evidence presented here.

Another feature linking fossil and modern apes is the presence of a frontal sinus in *P. major*. This is a feature shared only by *Pan* in living pongids and by hominids. It would seem to preclude *P. major* from being in any way ancestral to the orang-utan, and if it is found that the other Kenya dryopithecines also have frontal sinuses it would suggest that the orang-utan also had become differentiated at this time.

A third set of characters in the post-cranial morphology of *P. africanus* suggest that it was developing towards the condition seen in modern species of *Pan*. The distal extremity of the humerus in particular, and the dimensions of the deltoid crest and the size and robusticity of the radius all foreshadow the condition in *Pan* and are distinct from other species of primate. This is not to say that *P. africanus* was a knuckle-walker, but it does indicate that its morphology, and therefore perhaps its method of locomotion, had some of the prerequisites for developing knuckle-walking locomotion. Also in the post-cranial morphology, *D. macinnesi* has many features that might be expected in a gibbon ancestor. Particularly the long slender limb bones, the general lack of development of the muscular markings on the limb bones, and the rounded nature of the distal articular surface of the humerus, which lacks any prominent heels, all contribute to the gibbon-like appearance of the limb bones.

Pilbeam (1969) has concluded that because of the similarities between *P. major* and the gorilla they are on the same lineage, with the fossil ape directly ancestral to the gorilla. These similarities are listed by Pilbeam (1969 : 124) – marked sexual size dimorphism, males having large projecting canines and relatively prognathous faces, and trends towards the more lophodont and hypsodont molar of the male gorilla. These points of similarity are valid, but they are all size-related features, and it is likely that any large ape would have similar morphology. *Gigantopithecus* has some of these features but not others. In view of the time separating *P. major* from the present-day gorilla, these size-dependent features are poor evidence for substantiating an ancestor–descendant relationship between them. This is also true of the hypotheses put forward to link *P. africanus* with the chimpanzee.

It may be concluded, however, that the Kenya dryopithecines as a whole may have given rise to some of the living pongids, especially the African ones. There is no evidence other than that of size to connect any of the fossil species with any one of the living ones. Similarly the single hylobatid species *D. macinnesi* may have been ancestral to modern hylobatids as a whole.

Appendix I

Summary of exploration of East African Miocene Sites

Year	*Worker*	*Site*	*Description of material*
1909	R. Chesnaye, (C. W. Hobley), D. B. Pigott	Muhoroni, Koru and Karungu	Andrews 1911
1911	F. Oswald	Karungu	Oswald 1914, Andrews 1914
1926	H. L. Gordon	Koru	hominoid maxilla
1927	(E. J. Wayland)	Koru	2 hominoid incisors
1931	A. T. Hopwood	Koru	9 further hominoid specimens all described, Hopwood 1933a
1931–32	L. S. B. Leakey	Rusinga Island	several hominoids
	D. MacInnes	Songhor	2 hominoids, Keith 1932
1932	E. Nielsson	Koru	hominoid mandible

Year	*Worker*	*Site*	*Description of material*
1933	W. E. Owen	Ombo, Maboko, Mariwa, Majiwa, Uyoma	
	C. Arambourg	Losidok	Arambourg 1933
1934	V. E. Fuchs, D. MacInnes	Losidok	
	D. MacInnes	Maboko excavations Songhor	hominoid limb bones more hominoid fossils
1934–35	L. S. B. Leakey, P. E. Kent	Rusinga Island	more hominoid fossils Kent 1944
1938	D. MacInnes	Songhor	more hominoid fossils
1940	L. S. B. Leakey	Rusinga Island	more hominoid fossils
1942	L. S. B. Leakey	Rusinga Island	more hominoid fossils Leakey 1943, MacInnes 1943
1944	R. M. Shackleton	Maralal	Shackleton 1946
	F. Dixey	Loperot	Dixey 1944
1947	K. P. Oakley, D. M. A. Bate, J. Waechter, L. S. B. Leakey	Rusinga Island, Mfwangano Island	'further important Miocene fossils were found'; Clark & Leakey 1951 : 2
1947	British–Kenya Miocene Expedition	Rusinga Is.; visits to Mfwangano, Karungu, Koru, Uyoma	64 specimens of hominoids; Clark & Leakey 1951, and 6 not described
	R. M. Shackleton	Mtete Valley (Songhor)	
	D. MacInnes	Tambach, Maboko	1 specimen of hominoid
1948	University of California Expedition	Losidok, Moruorot	3 specimens of hominoid; Madden 1972
	British–Kenya Miocene Expedition	Rusinga Island Songhor	57 specimens of hominoid 48 specimens of hominoid; Clark & Leakey 1951, Clark & Thomas 1951
	L. S. B. Leakey	Loperot, new site at Koru	2 specimens of hominoid
1949	British–Kenya Miocene Expedition	Rusinga Island Mfwangano Island Songhor	21 specimens of hominoid 2 specimens of hominoid 31 specimens of hominoid
	L. S. B. Leakey	Kirimon Mbgathi	Clark & Leakey 1951 Clark 1952
	D. G. MacInnes	Maboko	
1950	British–Kenya Miocene Expedition	Rusinga Island Karungu Koru Mfwangano Songhor	69 specimens of hominoid 3 specimens of hominoid 4 specimens of hominoid 4 specimens of hominoid 6 specimens of hominoid; Clark 1952
1951	T. Whitworth	Rusinga Island at Gumba	Dryopithecine forelimb; Napier & Davis 1959
	British–Kenya Miocene Expedition	Rusinga Island Mfwangano	60 specimens of hominoid 2 specimens of hominoid; Whitworth 1953, Clark 1952
	L. S. B. Leakey, D. G. MacInnes	Moruorot, Losidok	3 specimens of hominoid

Year	*Worker*	*Site*	*Description of material*
1952	L. S. B. Leakey	Rusinga Island	12 specimens of hominoid
		Mfwangano	5 specimens of hominoid
1955	L. S. B. Leakey	Rusinga Island	2 specimens of hominoid
	T. Whitworth, R. J. G. Savage	Mfwangano	10 specimens of hominoid; Whitworth 1961
1956	Rosalie Osborn	Rusinga Island	33 specimens of hominoid
1958	L. S. B. Leakey	Rusinga Island	4 specimens of hominoid
1961	W. W. Bishop	Songhor	1 specimen of hominoid
1962	L. S. B. Leakey	Songhor	34 specimens of hominoid
1966	L. S. B. Leakey	Songhor	130 specimens of hominoid; Andrews 1970, 1974
1967	J. A. Van Couvering	Rusinga Island	4 specimens of hominoid; Leakey 1968
1968	J. A. Van Couvering	Rusinga Island	2 specimens of hominoid; Van Couvering & Miller 1969, Andrews 1974
1970	P. J. Andrews	Songhor	27 specimens of hominoid
1971	P. J. Andrews, J. A. Van Couvering	Rusinga Island	18 specimens of hominoid; Andrews & Van Couvering 1975
1972	P. J. Andrews	Songhor	30 specimens of hominoid
1973	D. R. Pilbeam, P. J. Andrews, J. A. Van Couvering	Maboko	10 specimens of hominoid
	P. J. Andrews	Karungu	

Appendix II

Summary of specimens available for study

	described	undescribed	Totals
D. macinnesi	49	111	160
P. (*R.*) *gordoni*	27	52	79
P. (*R.*) *vancouveringi*	1	9	10
L. legetet[1]	41	75	116
P. africanus[2]	73	45	118
P. nyanzae[3]	65	38	103
P. major[4]	19	34	53
Pongidae indet.	1	4	5
Totals	276	368	644

Detailed lists giving brief descriptions of the specimens assigned to each species, with their Museum collection numbers and published references, are deposited in the Palaeontology Library of the British Museum (Natural History).

[1] 57 additional specimens referred to this species, 20 from Fort Ternan and Maboko Island and 37 from Napak, Uganda.
[2] 2 additional specimens referred to this species from Fort Ternan.
[3] 6 additional specimens referred to this species from Fort Ternan.
[4] 28 additional specimens referred to this species, 24 from Napak and Moroto, Uganda, and 4 from Losidok, Moruorot and Kirimon.

Appendix III

List of specimen field numbers used by earlier workers with the equivalent permanent accession number used in this work. In addition to the field numbers, Pilbeam (1969) used a further set of numbers which put the field numbers roughly into numerical order. These are given in the first column. Examples of Pilbeam's numbering system are 1, CMH 1 and 271, 55.

Numerical order	Field no.	Permanent accession no.
1	CMH 1	KNM-RU 1674
	CMH 2	BM(NH) M 16647
5	CMH 3	KNM-RU 1677
4	CMH 4	KNM-RU 1676
6	CMH 5	KNM-RU 1678
	CMH 6	BM(NH) M 16649
7	CMH 7	KNM-RU 1679
8	CMH 8	KNM-RU 1680
	CMH 9	KNM-RU 1681
	CMH 10	KNM-RU 1685
	CMH 11	KNM-MB 104
	CMH 12	KNM-RU 1682
	CMH 13	KNM-RU 1684
	CMH 14	KNM-SO 373
	CMH 15	KNM-RU 1685
	CMH 16	KNM-RU 1686
	CMH 17	KNM-RU 1687
	CMH 18	KNM-RU 1688
	CMH 19	not primate
	CMH 20	lost
	CMH 21	KNM-RU 1690
	CMH 23	KNM-RU 1691
95	CMH 24	KNM-SO 375
	CMH 26	KNM-SO 942
	CMH 26	KNM-MB 107
	CMH 27	KNM-RU 1692
	CMH 28	KNM-RU 1747
	CMH 29	KNM-MB 108
23	CMH 30	KNM-RU 1694
24	CMH 31	KNM-RU 1695
25	CMH 32	KNM-RU 1696
	CMH 33	KNM-RU 1697
101	CMH 34	KNM-SO 381
102	CMH 35	KNM-SO 382
	CMH 36	KNM-SO 1086
	CMH 39	KNM-MB 125
	CMH 40	KNM-RU 1698
	CMH 41	KNM-RU 1699
	CMH 42	KNM-RU 1700
	CMH 43	KNM-RU 1701
	CMH 44	KNM-RU 1702
	CMH 45	KNM-RU 1749
	CMH 46	KNM-RU 1704
	CMH 47	KNM-SO 383
	CMH 48	lost
34	CMH 101	KNM-RU 1705
35	CMH 102	KNM-RU 1706
	CMH 103	KNM-RU 1707
	CMH 104	KNM-SO 385
	CMH 105	KNM-SO 386
	CMH 106	KNM-SO 387
	CMH 107	KNM-SO 388
	CMH 108	KNM-RU 1708
38	CMH 109	KNM-RU 1709
39	CMH 110	KNM-RU 1710
	CMH 111	KNM-RU 1711
41	CMH 112	KNM-RU 1712
	CMH 113	KNM-RU 1713
	CMH 114	lost
44	CMH 115	KNM-RU 1714
	CMH 116	KNM-RU 1715
	CMH 117	KNM-RU 1716
	CMH 118	KNM-RU 1717
	CMH 119	KNM-RU 1718
	CMH 120	KNM-RU 1719
50	CMH 121	KNM-RU 1720
	CMH 122	KNM-RU 1721
	CMH 123	KNM-RU 1722
	CMH 124	KNM-RU 1723
	CMH 125	KNM-RU 1724
	CMH 126	KNM-RU 1725
	CMH 127	KNM-RU 1726
	CMH 128	KNM-RU 1727
58	CMH 129	KNM-RU 1728
	CMH 130	not primate
	CMH 131	KNM-RU 1730
	CMH 132	KNM-RU 1731
	CMH 133	KNM-RU 1732
	CMH 134	KNM-RU 1733
64	CMH 135	KNM-RU 1734
65	CMH 136	KNM-RU 1735
	CMH 137	KNM-RU 1736
	CMH 138	KNM-RU 1737
	CMH 139	KNM-RU 1738
	CMH 140	KNM-RU 1739
	CMH 142	KNM-RU 1740
	CMH 143	KNM-RU 1741
	CMH 144	KNM-RU 1742
	CMH 147	KNM-RU 1743
	Rs C8	KNM-RU 1693
	72-41	KNM-RU 1758
113	F 3104	KNM-SO 391
	SH	KNM-SO 380
90	SD 4	KNM-SO 371
	S 5	KNM-SO 376
	S 5	KNM-SO 395
	S 13	KNM-SO 378
	S 15	KNM-SO 375
	S 17	KNM-SO 370
	S 19	KNM-SO 373
94	S 21	KNM-SO 374
	S 44	KNM-SO 384
	S 54	lost
91	S 9'38	KNM-SO 372
		KNM-SO 377
	1947 – Rusinga	
	60	KNM-RU 1762
	142	KNM-RU 1763
125	143	KNM-RU 1764
	144	KNM-RU 1765
129	257	KNM-RU 1767
	258	KNM-RU 1768
131	342	KNM-RU 1769
	503	KNM-RU 1773
	545	KNM-RU 1774
	546	KNM-RU 1775
	546	KNM-RU 1776
	593	KNM-RU 1778
	593	KNM-RU 2018
140	599	KNM-RU 1728
141	600	KNM-RU 1780
	602	KNM-RU 1781
144	603	KNM-RU 1782
	604	not primate

Appendix III (*cont.*)

Numerical order	Field no.	Permanent accession no.
147	645	KNM-RU 1785
	663	KNM-RU 1787
	667	KNM-RU 1788
151	683	KNM-RU 1789
	735	KNM-RU 1790
	684	KNM-RU 1791
	693	KNM-RU 1792
	710	BM(NH) M 16650
155	712	KNM-RU 1674
	746	KNM-RU 1795
	814	KNM-RU 1796
	843	KNM-RU 1797
	847	KNM-RU 1798
	908	KNM-RU 1799
	924	KNM-RU 1801
166	993	KNM-RU 1803
	994	KNM-RU 1804
	1011–1022	KNM-RU 1806
181	1043	KNM-RU 1818
	1047	KNM-RU 1806
183	1097	KNM-RU 1820
	1178	KNM-RU 1821
185	1228	KNM-RU 1822
186	1229	KNM-RU 1823
	1230	KNM-RU 1824
	1947 – Songhor	
190	1	KNM-SO 396
191	2	KNM-SO 397
	3	KNM-SO 398
	4	KNM-SO 399
	15	KNM-SO 401
196	16	KNM-SO 402
	17	KNM-SO 403
198	28	KNM-SO 404
	29	KNM-SO 405
	45	not primate
	80	BM(NH) M 16648
	105	KNM-SO 411
	1947 – Maboko	
	39	KNM-MB 109
	1948 – Rusinga	
	8	KNM-RU 1825
	27	KNM-RU 1826
1948	50	BM(NH) M 32363
	79	KNM-RU 1830
216, 48	80	KNM-RU 1831
218	103	KNM-RU 1833
220	138	KNM-RU 1835
	200	KNM-RU 1836
	205	KNM-RU 1837
	270	KNM-RU 1839
	276	KNM-RU 1840
	280	KNM-RU 1842
	334	KNM-RU 1667
	374 A	KNM-RU 1844
	B	KNM-RU 1850
	C	KNM-RU 1850
	D	KNM-RU 1847
	E	KNM-RU 1849
	F	KNM-RU 1849
	G	KNM-RU 1850
	G1	KNM-RU 1850
	G2	KNM-RU 1850
	374 H	KNM-RU 1849
	I	KNM-RU 1849
	J	KNM-RU 1849
	375	KNM-RU 1855
	394	not primate
	443	KNM-RU 1857
	444	KNM-RU 1858
	445	not primate
	446	KNM-RU 1860
	447	KNM-RU 1861
	571	KNM-RU 1862
262	635	KNM-RU 1864
	636	KNM-RU 1865
	637	KNM-RU 1664
	638	KNM-RU 1866
268	893	KNM-RU 1868
	893	KNM-RU 1869
	1948 – Songhor	
	1	KNM-SO 413
	7	KNM-SO 414
	52	KNM-SO 418
	53	KNM-SO 419
	54	lost
271	55	KNM-SO 415
272	56	KNM-SO 416
	57	KNM-SO 417
277	58	KNM-SO 420
	59	KNM-SO 421
	60	KNM-SO 422
	61	KNM-SO 423
	62	KNM-SO 424
	63	KNM-SO 425
	64	KNM-SO 426
	87	KNM-SO 428
	88	KNM-SO 429
	89	KNM-SO 430
	99	KNM-SO 434
	100	KNM-SO 435
	101	KNM-SO 436
	111	KNM-SO 441
301	112	KNM-SO 442
	120	KNM-SO 443
	121	KNM-SO 444
	122	KNM-SO 445
	123	KNM-SO 396
	404	KNM-SO 449
334	405	KNM-SO 450
	406	KNM-SO 451
	407	KNM-SO 462
	409	KNM-SO 452
	410	lost
	411	KNM-SO 453
	412	KNM-SO 454
	413	KNM-SO 455
	415	KNM-SO 457
	416	KNM-SO 458
	417	KNM-SO 459
	418	KNM-SO 460
	419	KNM-SO 461
	441	KNM-SO 462
	Sgr. '48	KNM-SO 561
	1948 – Koru	
	1	KNM-KO 6
	2	KNM-KO 7

Appendix III (*cont.*)

Numerical order	Field no.	Permanent accession no.
	1949 – Rusinga	
	73	KNM-RU 1870
	148	KNM-RU 1871
	155	KNM-RU 1872
	156	KNM-RU 1873
	278	KNM-RU 1874
	300	KNM-RU 1875
	516	KNM-RU 1876
	518	KNM-RU 1878
	519	KNM-RU 1650
	520	KNM-RU 1649
	541	KNM-RU 1880
	542	KNM-RU 1881
	605	KNM-RU 1882
	606	KNM-RU 1883
	649	KNM-RU 1887
374	692	KNM-RU 1889
	767	not primate
	769	KNM-RU 1666
	1949 – Mfwangano	
	64	KNM-MW 39
	65	KNM-MW 60
	1949 – Songhor	
380	1	KNM-SO 463
381	2	KNM-SO 464
382	3	KNM-SO 465
383	4	KNM-SO 466
384	5	KNM-SO 467
	6	KNM-SO 962
	7	KNM-SO 412
	11	KNM-SO 470
	12	KNM-SO 472
	13	KNM-SO 473
	14	KNM-SO 474
	15	KNM-SO 475
	16	KNM-SO 476
	245	KNM-SO 512
	246	KNM-SO 513
	247	KNM-SO 514
	307	KNM-SO 481
	308	KNM-SO 482
	309	KNM-SO 483
405	381	KNM-SO 485
406	382	KNM-SO 486
	384	KNM-SO 487
409	385	KNM-SO 488
	387	KNM-SO 489
	388	KNM-SO 490
	639	KNM-SO 506
	640	KNM-SO 507
	1950 – Rusinga	
	92	KNM-RU 1893
	93	KNM-RU 1894
507	94	KNM-RU 1895
	234	KNM-RU 1896
	280	KNM-RU 1897
	281	KNM-RU 1901
	282	KNM-RU 1899
	283–295	KNM-RU 1901
531	286	KNM-RU 1904
	296	KNM-RU 1914
	297	KNM-RU 1915
	298	KNM-RU 1916
	301	KNM-RU 1919
	302	KNM-RU 1920
	303	not primate
	448	KNM-RU 1922
538	486	KNM-RU 1923
539	487	KNM-RU 1924
	548	KNM-RU 1925
	582	KNM-RU 1926
542	583	KNM-RU 1927
	614	KNM-RU 1929
545	628	KNM-RU 1931
	669	KNM-RU 1932
547	670	KNM-RU 1933
	671	KNM-RU 1934
	748	KNM-RU 1935
550	777	KNM-RU 1936
	844	KNM-RU 1937
	878	KNM-RU 1928
	924	KNM-RU 1939
557	1040	KNM-RU 1942
560	1056	KNM-RU 1945
	1111	KNM-RU 1946
562	1145	KNM-RU 1947
	1185	KNM-RU 1948
	1335	KNM-RU 1949
566	1342	KNM-RU 1951
	1365	KNM-RU 1952
	1396	KNM-RU 1953
569	1403	KNM-RU 1954
570	1404	KNM-RU 1979
	1405	KNM-RU 1980
	1406	KNM-RU 1981
573	1558	KNM-RU 1955
	1559	KNM-RU 1956
	1592	KNM-RU 1957
	1681	KNM-RU 1671
	1756	KNM-RU 1958
578	1775	KNM-RU 1959
	1798	KNM-RU 1960
	1814	KNM-RU 1962
	1815	KNM-RU 1963
	1816	KNM-RU 1964
	1817	KNM-RU 1965
	1854	KNM-RU 1966
	1900	KNM-RU 1968
	1901	KNM-RU 1969
	1915	KNM-RU 1970
	1985	KNM-RU 1971
	1986	KNM-RU 1972
	1987	KNM-RU 1973
593	1988	KNM-RU 1974
594	1989	KNM-RU 1975
	1991	KNM-RU 1977
	2003	KNM-RU 1857
	1950 – Songhor	
	2	KNM-SO 927
	3	KNM-SO 928
	4	KNM-SO 929
	70	KNM-SO 516
	71	KNM-SO 517
	1950 – Mfwangano	
	3	KNM-MW 40
	4	KNM-MW 41
	5	KNM-MW 42
	2	KNM-MW 61

Appendix III (*cont.*)

Numerical order	Field no.	Permanent accession no.
	1950 – Karungu	
	21	KNM-KA 5
	24	KNM-KA 6
	25	KNM-KA 7
	1950 – Koru	
	1	KNM-KO 8
618	2	KNM-KO 9
	1 A	KNM-KO 11
	1951 – Rusinga	
620	1	KNM-RU 1982
	77	KNM-RU 1984
	111	KNM-RU 1985
	112	KNM-RU 1986
	176	KNM-RU 1988
	177	KNM-RU 1989
	178	KNM-RU 1990
	179	KNM-RU 1991
	180	KNM-RU 1992
	181	KNM-RU 1993
	182	KNM-RU 1994
	183	KNM-RU 1995
	184	KNM-RU 1996
	259	KNM-RU 1998
637	260	KNM-RU 1999
	346	KNM-RU 2000
	409	KNM-RU 2001
	417	KNM-RU 2002
	493	KNM-RU 2003
	505	KNM-RU 2004
	538	KNM-RU 2005
	539	KNM-RU 2007
	543	KNM-RU 2008
	560	KNM-RU 2009
	590	KNM-RU 2010
	591	KNM-RU 2011
	592	KNM-RU 2012
	593	KNM-RU 2013
	636	KNM-RU 2015
	706	KNM-RU 2016
	707	KNM-RU 2017
	708	KNM-RU 2018
	709	KNM-RU 2019
	711	KNM-RU 2020
	716	KNM-RU 2021
	725	KNM-RU 2023
	738	KNM-RU 2024
	749	KNM-RU 2025
	774	KNM-RU 2026
	807	KNM-RU 2027
	808	KNM-RU 2028
	809	KNM-RU 2028
	1087	KNM-RU 2030
	1100	KNM-RU 2038
	1158	KNM-RU 2037
	1243	KNM-RU 2031
	1244	KNM-RU 2032
	1245	KNM-RU 2033
	1376	KNM-RU 2034
	1435	KNM-RU 2035
51	1499	KNM-RU 2036
	1951 – Losidok	
	5	KNM-LS 1

After 1951, specimens described by Pilbeam (1969) for the first time.

R 686,313	KNM-RU 2041	Sgr. 1′62	KNM-SO 396
R 688,315	KNM-RU 2043 (lost)	Sgr. 139′62	KNM-SO 521
R 690,317	KNM-RU 2045	Sgr. 143′62	KNM-SO 522
R 694,2542	KNM-RU 2049	Sgr. 144′62	KNM-SO 523
R 715,156	KNM-RU 2051	Sgr. 145′62	KNM-SO 524
R 722,550	KNM-RU 2061	Sgr. 8′62	KNM-SO 528

References

Allbrook, D. & Bishop, W. W. 1963. New fossil hominoid material from Uganda. *Nature, Lond.* **197**: 1187–1190.

Andrews, C. W. 1911. On a new species of *Deinotherium* (*D. hobleyi*) from British East Africa. *Proc. zool. Soc. Lond.* **1911**: 943, pl. 48.

—— 1914. On the Lower Miocene vertebrates from British East Africa, collected by Dr Felix Oswald. *Q. Jl geol. Soc. Lond.* **70**: 163–186, pls 27–29.

Andrews, P. J. 1970. Two new fossil primates from the Lower Miocene of Kenya. *Nature, Lond.* **228**: 537–40.

—— 1973. *Miocene primates* (*Pongidae, Hylobatidae*) *of East Africa.* xix+511+x pp., 82 figs. Ph.D. thesis, University of Cambridge.

—— 1974. New species of *Dryopithecus* from Kenya. *Nature, Lond.* **249**: 188–190, 680.

——, **Groves, C. P. & Horne, J. F. M.** 1975. Ecology of the Lower Tana River flood plain (Kenya). *Jl E. Afr. nat. Hist. soc. natn. Mus.*, Nairobi, **151**: 1–31, 3 figs.

—— **& Simons, E. L.** 1977. A new African Miocene gibbon-like genus, *Dendropithecus* (Hominoidea, Primates) with distinctive postcranial adaptations: its significance to the origin of Hylobatidae. *Folia primatol.*, Basel, **28**: 161–168.

—— **& Tobien, H.** 1977. A new Miocene locality in Turkey with evidence on the origin of *Ramapithecus* and *Sivapithecus. Nature, Lond.* **268**: 699–701.

—— & **Van Couvering, J. A. H.** 1975. Palaeoenvironments in the East African Miocene. *In* Szalay, F. S. (ed.), *Approaches to Primate Paleobiology*: 62–103, 3 figs. Basel.

—— & **Williams, D. B.** 1973. The use of principal components analysis in physical anthropology. *Am. J. phys. Anthrop.*, Washington, **39**: 291–304.

Arambourg, C. 1933. Mammifères Miocénes du Turkana. *Annls Paléont.*, Paris, **22**: 123–147, pls 12–13.

Bishop, W. W. 1964. More fossil primates and other Miocene mammals from north-east Uganda. *Nature, Lond.* **203**: 1327–1331.

——, **Miller, J. A. & Fitch, F. J.** 1969. New potassium–argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *Am. J. Sci.*, New Haven, **267**: 669–699.

Bonis, L. de, Bouvrain, G., Geraads, D. & Melentis, J. 1974. Première découverte d'un Primate hominoide dans le Miocène supérieur de Macédoine (Grèce). *C.r. hebd. Séanc. Acad. Sci., Paris* **278** (D): 3063–3066.

Blyth, E. 1875. Catalogue of mammals and birds of Burma. *J. Asiat. Soc. Beng.*, Calcutta, **44**. xiv + 167 pp.

Booth, A. H. 1956. The Cercopithecidae of the Gold and Ivory Coasts: geographic and systematic observations. *Ann. Mag. nat. Hist.*, London, (12) **9**: 476–480.

—— 1957. Observations on the natural history of the Olive Colobus monkey (*Procolobus verus*). *Proc. zool. Soc. Lond.* **129**: 421–430.

—— 1958. The zoogeography of West African primates: a review. *Bull. Inst. fr. Afr. noire*, Dakar, **20** (A): 587–622.

Cave, A. J. E. 1961. The frontal sinus of the gorilla. *Proc. zool. Soc. Lond.* **136**: 359–373, pl. 1.

—— & **Haines, R. W.** 1940. The paranasal sinuses of the anthropoid apes. *J. Anat.*, London, **74**: 493–523, 21 figs.

Chesters, K. I. M. 1957. The Miocene flora of Rusinga Island, Lake Victoria, Kenya. *Palaeontographica*, Stuttgart, **101** (B): 30–67, pls 19–21.

Clark, W. E. le Gros 1950. New palaeontological evidence bearing on the Hominoidea. *Q. Jl geol. Soc. Lond.* **105**: 224–264, pls 11–15.

—— 1952. Report on fossil hominoid material collected by the British–Kenya Miocene expedition. *Proc. zool. Soc. Lond.* **122**: 273–286, pls 1–3.

—— & **Leakey, L. S. B.** 1950. Diagnoses of East African Miocene Hominoidea. *Q. Jl geol. Soc. Lond.* **105**: 260–262.

—— —— 1951. The Miocene Hominoidea of East Africa. *Fossil Mammals Afr.*, London, **1**. v + 117 pp., 28 figs, 9 pls.

—— & **Thomas, D. P.** 1951. Associated jaws and limb bones of *Limnopithecus macinnesi*. *Fossil Mammals Afr.*, London, **3**. 27 pp., 8 figs, 6 pls.

Delson, E. 1973. *Fossil colobine monkeys of the circum-Mediterranean region and the evolutionary history of the Cercopithecidae* (*Primates, Mammalia*). iv + 856 pp., 125 figs. Ph.D. thesis, Columbia University, New York.

—— & **Andrews, P. J.** 1975. Evolution and interrelationships of the catarrhine Primates. *In* Luckett, W. P. & Szalay, F. S. (eds), *Phylogeny of the primates, an interdisciplinary approach*: 405–446. New York.

Dixey, F. 1944. Miocene sediments in south Turkana. *Jl E. Africa nat. Hist. Soc.*, Nairobi, **18**: 13–14.

Dorst, J. & Dandelot, P. 1970. *A field guide to the larger mammals of Africa*. 287 pp., 44 pls. London.

Elliot, D. G. 1913. A review of the primates. *Monogr. Am. Mus. nat. Hist.*, New York, **1**. cxxvi + 317 + xxxviii pp., 32 pls. **2**. xviii + 382 + xxv pp., 39 pls. **3**. xiv + 262 + clxvii pp., 39 pls.

Every, R. G. 1970. Sharpness of teeth in man and other primates. *Postilla*, New Haven, **143**. 30 pp., 5 figs.

Fleagle, J. 1975. A small gibbon-like hominoid from the Miocene of Uganda. *Folia primatol.*, Basel, **24**: 1–15.

Freedman, L. 1957. The fossil Cercopithecoidea of South Africa. *Ann. Transv. Mus.*, Pretoria, **23**: 121–262, 7 figs, 53 pls.

Frisch, J. E. 1965. Trends in the evolution of the hominoid dentition. *Biblthca primatol.*, Basel, **3**: 1–130, 27 figs.

Goodman, M. G. 1968. *Structure and function in the symphyseal region of the pongid mandible*. 216 pp., 38 figs. Ph.D. thesis, Yale University, New Haven.

Gray, J. E. 1825. An outline of an attempt at the disposition of mammalia into tribes and families, with a list of the genera apparently appertaining to each tribe. *Ann. Phil.*, London, **10**: 337–344.

Greenfield, L. O. 1972. Sexual dimorphism in *Dryopithecus africanus*. *Primates*, Inuyama City, Japan, **13**: 395–410.

Gregory, W. K. & Hellman, M. 1939. The dentition of the extinct South African man-ape *Australopithecus* (*Plesianthropus*) *transvaalensis* Broom. A comparative and phylogenetic study. *Ann. Transv. Mus.*, Pretoria, **19** (4): 339–373, 14 figs.

Groves, C. P., Andrews, P. J. & Horne, J. F. M. 1974. Tana River Colobus and Mangabey. *Oryx*, London, **12** : 565–575.

Hopwood, A. T. 1933. Miocene primates from British East Africa. *Ann. Mag. nat. Hist.*, London, (10) **11** : 96–98.

—— 1933a. Miocene primates from Kenya. *Zool. J. Linn. Soc.*, London, **38** : 437–464, pl. 6.

Keay, R. W. J. 1959. *Vegetation Map of Africa south of the Tropic of Cancer* (explanatory notes). 24 pp., 1 map col. London.

Keith, A. 1932. Human Palaeontology, Africa. *Man*, London, **32** : 208.

Kent, P. E. 1944. The Miocene beds of Kavirondo, Kenya. *Q. Jl geol. Soc., Lond.* **100** : 85–118.

Kingdon, J. 1971. *East African mammals, an atlas of evolution in Africa*, **1**. x + 446 pp. London.

Korenhof, C. A. W. 1960. *Morphogenetical aspects of the human upper molar*. 368 pp., 60 figs, 15 pls. Utrecht.

Lartet, E. 1856. Note sur un grand singe fossile qui se rattache au groupe des singes supérieurs. *C.r. hebd. Séanc. Acad. Sci., Paris* **43** : 210–223, 1 pl.

Leakey, L. S. B. 1943. A Miocene anthropoid mandible from Rusinga, Kenya. *Nature, Lond.* **152** : 319–320.

—— 1967. An early Miocene member of Hominidae. *Nature, Lond.* **213** : 155–163.

—— 1968. Lower dentition of *Kenyapithecus africanus*. *Nature, Lond.* **217** : 827–830.

—— **& Clark, W. E. le Gros** 1955. British–Kenya Miocene Expeditions. *Nature, Lond.* **175** : 234.

Lewis, O. J. 1970. Evolution of the hominoid wrist. *In* Tuttle, R. H. (ed.), *The functional and evolutionary biology of primates* : 207–222. Chicago.

—— 1971. Brachiation and the early evolution of the hominoidea. *Nature, Lond.* **203** : 577–579.

—— 1972. Osteological features characterizing the wrists of monkeys and apes with a reconsideration of this region in *Dryopithecus* (*Proconsul*) *africanus*. *Am. J. phys. Anthrop.*, Washington, **36** : 45–58.

MacInnes, D. G. 1943. Notes on the East African Miocene primates. *Jl E. Africa nat. Hist. Soc.*, Nairobi, **17** : 141–181.

Madden, C. T. 1972. Miocene mammals, stratigraphy and environment of Moruorot Hill, Kenya. *Paleobios*, Berkeley, **14**. 12 pp.

Morbeck, M. E. 1975. *Dryopithecus africanus* forelimbs. *J. hum. Evol.*, London, **4** : 39–46.

Napier, J. R. & Davis, P. R. 1969. The fore-limb skeleton and associated remains of *Proconsul africanus*. *Fossil Mammals Afr.*, London, **16**. x + 69 + vi pp., 16 figs, 10 pls.

Oswald, F. 1914. The Miocene beds of the Victoria Nyanza, and the geology of the country between the Lake and the Kisii Highlands. *Q. Jl geol. Soc. Lond.* **70** : 128–162, pls 20–26.

Ozansoy, F. 1955. Sur les gisements continentaux et les mammifères du Néogène et du Villafranchien d'Ankara (Turquie). *C.r. hebd. Séanc. Acad. Sci., Paris* **240** : 992–994.

—— 1957. Faunes des mammifères du Tertiaire de Turquie et leurs revisions stratigraphiques. *Bull. Miner. Res. Explor. Inst. Ankara* **49** : 29–48.

Pilbeam, D. R. 1969. Tertiary Pongidae of East Africa: evolutionary relationships and taxonomy. *Bull. Peabody Mus. nat. Hist.*, New Haven, **31** : 1–185, 31 figs.

—— **& Walker, A. C.** 1968. Fossil monkeys from the Miocene of Napak, north-east Uganda. *Nature, Lond.* **220** : 657–660.

Preuschoft, H. 1973. Body posture and locomotion in some East African Miocene Dryopithecinae. *In* Day, M. H. (ed.), Human Evolution. *Symp. Soc. Stud. hum. Biol.*, London, **11** : 13–46, 20 figs.

Rahm, U. 1965. Distribution et écologie de quelques mannifères de l'est du Congo. *Zoologica afr.*, Cape Town, **1** : 149–164.

Schlosser, M. 1911. Beiträge zur Kenntnis der oligozänen Landsäugetiere aus dem Fayum, Ägyptem. *Beitr. Paläont. Geol. Ost.-Ung.*, Vienna, **24** : 51–167.

Schuman, E. L. & Brace, C. L. 1954. Metric and morphologic variations in the dentitions of the Liberian chimpanzee; comparisons with anthropoid and human dentitions. *Hum. biol.*, Detroit, **26** : 239–268.

Shackleton, R. M. 1946. Geology of the country between Nanyuki and Maralal. *Rep. geol. Surv. Kenya*, Nairobi, **11** : 1–54.

Simons, E. L. 1963. A critical reappraisal of Tertiary primates. *In* Buettner-Janusch, J. (ed.), *Genetic and evolutionary biology of the primates* : 65–129. New York.

—— 1965. New fossil apes from Egypt and the initial differentiation of Hominoidea. *Nature, Lond.* **205** : 135–139.

—— 1967. The earliest apes. *Scient. Am.*, New York, **217** : 28–35.

—— 1967a. The significance of primate paleontology for anthropological studies. *Am. J. phys. Anthrop.*, Washington, **27** : 307–322.

—— 1969. Miocene monkey (*Prohylobates*) from northern Egypt. *Nature, Lond.* **223** : 687–698.

—— 1971. A current review of the interrelationships of Oligocene and Miocene Catarrhini. *In* Dahlberg, A. A. (ed.), *Dental morphology and evolution* : 193–208. Chicago.
—— & **Pilbeam, D. R.** 1965. Preliminary revision of the Dryopithecinae (Pongidae, Anthropoidea). *Folia primatol.*, Basel, **3** : 81–152.
—— —— 1972. Hominoid Paleoprimatology. *In* Tuttle, R. H. (ed.), *The functional and evolutionary biology of primates* : 36–62. Chicago.
Simpson, G. G. 1931. A new classification of mammals. *Bull. Am. Mus. nat. Hist.*, New York, **59** : 259–293.
Trevor, J. 1950. Anthropometry. *Chambers' Encyclopaedia* : 458–462. London.
Van Couvering, J. A. & Miller, J. A. 1969. Miocene stratigraphy and age determinations, Rusinga Island, Kenya. *Nature, Lond.* **221** : 628–632.
Verdcourt, B. 1963. The Miocene non-marine mollusca of Rusinga Island, Lake Victoria and other localities in Kenya. *Palaeontographica*, Stuttgart, **121** (A) : 1–37, 64 figs.
—— 1972. The zoogeography of the non-marine mollusca of East Africa. *J. Conch. Lond.* **27** : 291–348.
Whitworth, T. 1953. A contribution to the geology of Rusinga Island. *Q. Jl geol. Soc. Lond.* **109** : 75–96.
—— 1961. The geology of Mfwanganu Island, western Kenya. *Overseas Geol. Miner. Resour.*, London, **8** : 150–190.
Wolpoff, M. H. 1971. Interstitial wear. *Am. J. phys. Anthrop.*, Washington, **34** : 205–228.
Zapfe, H. 1960. Die Primatenfunde aus der miozänen Spaltenfüllung van Neudorf an der March (Devinska Nova Ves). Tschechoslowakei. *Schweiz. palaeont. Abh.*, Basel, **78** : 1–293, 115 figs.
Zingeser, M. R. 1969. Cercopithecoid canine tooth honing mechanisms. *Am. J. phys. Anthrop.*, Washington, **31** : 205–214.

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